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LIVING MACHINERY

Eight Lectures Delivered at
The Lowell Institute, Boston, March, 1927

BY

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TO

MY FOUR ASSISTANTS

AND

EXPERIMENTAL SUBJECTS:

POLLY, DAVID, JANET, AND MAURICE:

FOR THEIR UNFAILING ZEAL AND

CO-OPERATION

difficult for me to lecture for six whole hours on this subject, and I foresaw that demonstrations and experiments on it might lead to ill-feeling. Were I to use my own family only for experiments on how to taste things (presumably good things) it might make the rest of my audience jealous and the family sick. If I carried out the experiments on the whole of the audience it might make the Royal Institution bankrupt.

So I had to think the matter out for myself and I decided to talk on something very ordinary, our nerves and muscles, how we feel what is going on inside and around us and how we move ourselves about.

Once a decision had been made the family expressed a lively interest in the matter. (I must remark that they sometimes come to the Laboratory with me to "help," and that David was there when I first succeeded in measuring the heat produced by nerves.) Of their suggestions, the best one came from Janet, aged 8, who proposed that I should make experiments upon her, a proposal seized upon at once by the rest, with results which later were witnessed at the Royal Institution.

The more I thought about it, the better it seemed. Fearful experiments I would make: Polly's heart (aged 12) should be shown beating, her lungs should be measured up, perhaps even her bones should be

shown, her emotions should be exposed on a screen: David should be given electric shocks till sparks came out of his hands, he should climb to the top of Monte Rosa and pedal a bicycle there (a strange place to find a bicycle) till exhausted, then he should be given oxygen and feel fresh again at once. Janet should have the movements of her stomach (there is no decency in young ladies these days) shown to the audience on a screen. Then the noises made by Maurice's heart (aged 7) should be made to resound like a gun all round the lecture hall; he should breathe strange gases out of a bag, and he would not be content till I had promised that he also should have electric shocks. Alas, not all of this could be done, but some of it could.

It is extraordinary how little most people know about their own bodies. Only at the age of sixteen from a classical headmaster did I learn that muscle is the red meat and not the gristle, and I often imagined that my heart must be wrong because I could hear it beating. Again, in common with most boys, I had the most ridiculous notions about "training"; drink as little as possible, don't eat potatoes or pastry, take a spoonful of some wonderful patent food after each meal. It is the same with other machines. Many people who own automobiles know very little about the insides of them and how they work; which is distressing enough, especially when

they go wrong. How many more who own perfectly good bodies haven't the vaguest idea of their machinery, or of the meaning and importance of their various parts! In these six Christmas lectures I would try to give my audience some idea of the working of two of the most important parts of the body: the muscles which move it about and the nerves which arrange where and how it shall be moved. If they began to understand these they would know enough to make them want to understand many other things too. They might even become physiologists later on, and join us in our gay adventure of trying to find out about the nature of living things. After all, they and their successors would discover much more than I could ever hope to do: so even if it wasted a little time (and as a matter of fact it wasted a good deal of time) it might be worth while.

About the time that this was all decided, and the plan of campaign laid, another invitation came, this time from President Lowell, to give a course of Lectures at the Lowell Institute at Boston. Of course I wanted to come—was not Harvard University founded by John Harvard of Emmanuel, and were there not more physiologists and other congenial souls to the square yard at Boston and Cambridge, Massachusetts, than in any other place outside Cambridge, England?—but what on earth

should I lecture about? To make eight more lectures, after exhausting all I had to say on the children at the Royal Institution, seemed an impossible task. Again I needed advice; and I turned this time to my wife. Her opinion on this matter was just as emphatic as that of my children on the other one. Why not give them the same lectures? Why make up eight new uninteresting lectures for the people of Boston, when all the interesting things had already been told to the children in London. This did seem rather unfair, and I decided to accept President Lowell's invitation, and to adopt her solution of the difficulty.

The Lectures to a Juvenile Auditory at the Royal Institution are established by old and sacred custom. On other occasions the passages and stairways there are covered with soft carpets: at Christmas time these are removed, as they were in the days of Faraday, to allow for the dirty boots of school boys tramping to the lectures through the muddy lanes of Piccadilly and Albemarle Street. The lectures are experimental: even if one prepares them beforehand in writing one knows, perfectly well, that one will say something quite different on the actual day. The audience charges down, at the end of each lecture, and insists on seeing the experiments again at close quarters. If one asks for an assistant in an experiment—or even for an "experimental animal"—

there is a rush of volunteers. Grown up people—hundreds of them—come to these lectures: one may discover distinguished statesmen, scholars, and scientists, disguised as uncles, parents, and grandparents: sometimes even without any reasonable excuse. It is assumed, if they come, that they do so at their own risk: no particular notice is taken of them: they are given the temporary rank of "Juveniles," "for the period," as we used to say during the War. They are not allowed to ask any stupid and grown-up questions: they must fulfil the obligations of their temporary rank.

Now this is all very well in London during Christmas time, but such lectures as these on the machinery of the body, if given in cold blood, formally, and without the gaiety of Christmas and the glamour of experimental demonstration, to a grown up audience in Boston would inevitably raise questions of a scientific and philosophical nature, to which the answer "Don't be stupid and grown-up" would be inadequate. There is of course no doubt that in many respects the human body behaves like a machine: its behaviour can be expressed in engineering terms: the muscles of a first-class sprinter may be developing 8 horse-power of mechanical energy while he is running a hundred yards: even in an ordinary person, like a Lowell Lecturer, they may develop 5 horse-power for a few seconds. The nervous sys-

tem carries out its duties like an automatic telephone exchange. The heart does enough work in 65 years to lift the whole body clean away into space, out of the gravitational field of the earth. There is no doubt at all of this machinery: work, energy, combustion, heat, electrical potentials, electric waves, messages switched through from one exchange to another, all remind one of the electrical and mechanical devices with which the modern world is filled. Deep, however, in the human mind is a repugnance to accept such a simple mechanical view. What is the basis of the belief that physiology can discover and lay bare the ultimate machinery of the body—if indeed it be machinery? What tools does it use? How is it related to the other sciences? Has it need of any concepts other than theirs? Is there any place in this modern materialistic physiology for the conception of life and consciousness, which after all are the things, beyond all others, of which, as observers of Nature, we are really certain? Are "purpose," "function," "adaptation" merely by-products of evolution by natural selection, working in a world governed only by the laws of physics and chemistry? Such questions inevitably arise in the minds of grown up people listening to a lecturer discoursing on "Living Machinery." He would be lacking in honesty were he not to try to face them for himself: he would be lacking in courage were he un-

willing to discuss them with his audience. Something clearly had to be done about it, or his job would seem unfinished: and I decided that at the end of the six lectures in which I would describe the machinery of the body, frankly and objectively, I would give two other lectures on "The Place of Physiology among the Sciences" and on "Mechanism and Purpose," in which these much more difficult and fundamental questions would be raised.

To the scholar or the philosopher perhaps these general matters may seem easy to debate: to the experimental scientist such discussion is very difficult because decision by an appeal to Nature is impossible, and he is apt to recognise the authority of no other court. Yet, it is good for him to make the attempt, to try to see the place of his science and his work in relation to other facts of life, however incapable of measurement and exact description these may be. In the first six lectures, therefore, I have tried to deal objectively with certain aspects of the machinery of the body—for machinery, to my mind, it unquestionably is—and in the last two—especially in the last of all—I have attempted, very diffidently, not to answer—for I am not sure that there is an answer!—but to comment on certain of the problems which are inevitably raised by such objective treatment of life-phenomena. In the first six lectures I have discussed some of the wonderful mechanisms

of the living body: in the seventh I have described how other sciences have aided, and will aid in their discovery and investigation: in the last I have disowned a purely mechanistic view of them, and tried to give, not a philosophy, not, alas, even a consistent picture, but a point of view not uncommon, though generally unexpressed, among those who, studying the phenomena and mechanisms of life, attempt occasionally to view them as a whole.

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LIVING MACHINERY

LECTURE I

Nerves and the Messages they Carry

If we take a dead frog and skin it, and pull the tissues of its leg apart, we shall find a little white thread—the sciatic nerve—running down from its backbone to the muscles of its calf. Plate I, *a* shows some of the nerves of the human arm, which are much the same, only longer and often thicker. If the frog has not been dead too long its leg will kick when we pinch or cut the nerve. If we take the nerve out carefully, leaving a muscle joined to it (fig. 1), we can experiment with it for hours and days, which is one reason why we know so much about it. This nerve is "alive," and remains alive for some time after its previous owner is dead. You will ask: How do we know that it is alive? How can a nerve be alive when its owner is dead? All of us, some time or other, have asked that question, especially those of us who are physiologists, and there is no complete answer to it, because no one knows exactly what he means by "live" and "dead"; but as we learn more about the body, and about living things in general, we find that the body is like an army containing millions of soldiers; the

army may be beaten and dispersed, may cease indeed to exist as an army, but the individual soldiers of it will not necessarily die when this calamity occurs; most of them will live for a time, some for a long time, after the defeat. Just so it is with the frog that has-been killed: many of his parts will go on working exactly as they did when the frog was certainly alive. That is all, or nearly all, we mean by saying that they are "alive." The nerve will continue sending messages to and fro, which is its proper job in life, just the same as when it was embedded under the muscles of the leg. It will not last, of course, for ever; its messages become weaker and weaker, and finally stop altogether, and nothing can then start them going again. Now the nerve is dead. But the fact that it works so well, and so long, before it dies is the reason why we can experiment with it, and why we know so much about it.

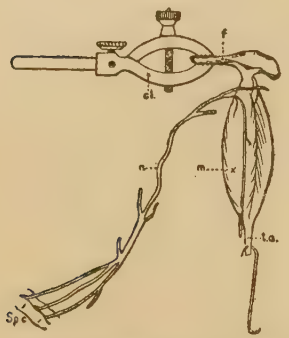


FIG. 1.—"Muscle nerve preparation" from a frog. The bone (*femur*) is held in a clamp (*cl.*), and the calf muscle (gastrocnemius) attached to it has a hook passed through its tendon (*t.a.*), by which its movements can be measured and recorded. This nerve (*n.*) running out by three roots from the spinal canal (*sp.c.*) is dissected out down to the place where it enters the muscle, all the branches being cut except those supplying the muscle (Foster).

If we look at a nerve under a microscope, we find that it is made up of hundreds of long and very fine fibres, each about $\frac{1}{10}$ as thick as a human hair,

Plate I, *b* shows a section across one of the bundles of the sciatic nerve; Plate I, *c* the same, but with a much higher magnification. In the nerves with which we feel, or by which we send messages to our muscles (there are others which are different), each of these fibres has a covering and an inside, just like an insulated electric wire. If we follow these fibres up we find that each of them runs the whole way along the nerve, from the place where it starts inside the spinal column to the place where it ends in the muscle or on the surface of the body. These nerve-fibres are branches, or "processes," of living "cells." Each cell is an individual soldier of the army, having his proper place in the company of his fellows, either in what we call the "spinal cord," or in those higher parts of the "nervous system" which are hidden away, for safety, inside the skull. Plate II, *b* is a highly magnified picture of a nerve-cell of the human brain; Plate II, *c* a similar picture of a "motor" nerve-cell (*i.e.* one which sends orders to the muscles) of the spinal cord. The nerve-cells communicate with each other in all directions: they receive and transmit messages from the outside or the inside; they send messages to the muscles, along the nerve-fibres which form part of them; they are separate living things, but they dwell in very close community with one another and go to make up the army of cells which we know as an "animal."

When animals first started long ago they were small, and were not in much of a hurry. If one part wanted to communicate with another part it did so, so to speak, through the post and not by sending a telegram. It released some substance; it posted a letter, as it were, which went wandering round in the fluids of the body until it came to a place where its message could be delivered. This method is still used. For example, when we run upstairs and need more oxygen to provide energy for the work, we make carbonic acid and lactic acid in our muscles, which travel round in the blood until they come to a corner of the brain (the "respiratory centre") where they deliver their message, the nervous system sends orders to the respiratory muscles, and we begin to breathe more deeply. Or again, when the food in the stomach passes on for further digestion, it acts upon the wall of the intestine with which it comes in contact, and thus sets free a messenger substance called "secretin": this wanders round in the blood until it gets to an organ called the pancreas, which immediately starts to pour out the ferments required to continue the good work of digestion. Sending things through the post, however, may be very slow, and as animals developed they found it necessary to invent a quicker method of passing messages from one part of the body to another, just as we have invented telegraphs and

telephones and wireless. And the method they invented was that of using a nerve, a little, long, unbroken living pathway along which "impulses" (as they are called) can run from one place to another.

It used to be believed that the nerves were hollow, and that a fluid like water ran along them and blew up the muscles to which they were connected. In fact, however, nothing material runs along them, any more than along an electric wire, or through the space which is filled with wireless waves; nor do the muscles get larger when they "contract," indeed, they become a very little smaller. When sound travels through the air nothing material goes with it. When a ripple passes over water, the water does not flow in the direction of the ripple. When one takes a rope and shakes it, a wave may move along it, but the rope does not move too. When a wave of wind travels across a cornfield, the corn itself remains where it was. So, in a nerve, a wave travels, but a wave of nothing material, just a *wave of change* occurring in the substance of the nerve. If you want to understand present-day physics, or engineering, or even physiology, you must acquire this notion of the passage of a wave. Waves turn up everywhere—in sound, in light, in wireless; and they turn up hundreds of thousands of times a second in an active nervous system.

These nerve-fibres are arranged in just the same

way as the wires of a telephone system. Each little muscle-fibre, each little sensory organ by which we feel is connected with its own nerve-fibre, just as we in our houses are supplied each with a single telephone line. Fig. 2, for example, shows certain end-organs in the skin, each connected to its own

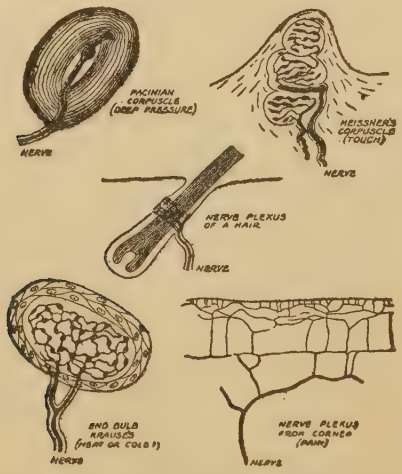


FIG. 2.—End-organs in the skin, each attached to its own nerve-fibre (Starling).

nerve-fibre; the various sensations which they arouse are given. The stimulation of a minute area of the skin will not excite *all* these sensations, but only one of touch or pain, or of cold or warmth, depending on which kind of end-organ is nearest to the point stimulated. These end-organs are much more frequent in some parts of the body than in others: for example, there are thirty times as many "touch spots" to a given area of skin in the tip of the

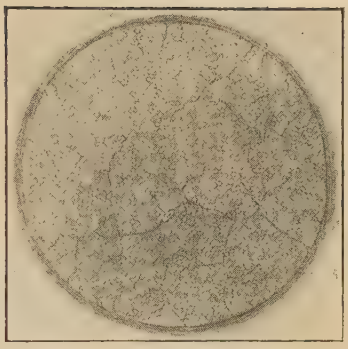
finger as in the upper arm. We *recognise* the sensation by noting which particular kind of end-organ it comes from, and *localise* it by noting which particular *one* of that kind is being excited. The cornea of the eye has no end-organs except those of pain, consequently any sensations from it, however weak, will be painful. In general, each kind of stimulus excites only its particular end-organ. If it be excessive it may excite others: for example, a very hot bath may stimulate not only the organs sensitive to heat, but those that respond to touch, with the result that we feel an intense tickling sensation.

To return once more to the analogy of the telephone system, every part of the body is not *directly* connected to every other part, just as subscribers are not all *directly* connected together by their telephone wires; there is a system of "exchanges" by which any subscriber can be put through to any other. In the case of the body, these "exchanges" are in what we call the "nervous system"—that is, in the brain and spinal cord. In Plate II, *a* are shown the brain and spinal cord of a man, as they would appear if the back of the skull and the back of all the vertebræ were removed. At the top are the cerebrum and cerebellum, each divided into a right and left half; below is the spinal cord, showing the "roots" of the nerves running out. The cord is made up of two parts—an inner portion of "grey" matter, which

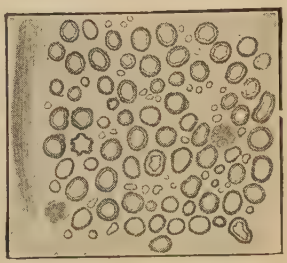
consists of the nerve-cells; and an outer portion of "white" matter, which consists of the nerve-fibres running up and down. Messages are transmitted in the outer "white" portion; the "exchanges" are in the inner "grey" portion. The action of these exchanges is largely automatic, just like that of an automatic telephone, which is much quicker than an ordinary one. If we flash a light in a man's eyes, he blinks; if we make a bang, he jumps; if we tap him, as he is sitting with legs crossed, just below the knee-cap, his leg kicks forward, quite independently of whether he wants it to or not. A particular set of messages has been sent: they get to the exchange, they pass, perhaps, to other exchanges, all automatically, and in a few thousandths of a second they call up the muscles which make the blink, or jump, or kick.

There are millions of nerve-fibres in the body, running to every point on the surface and to many points inside it. This method of using exchanges saves an enormous number of lines, as it does with our telephone system. If every part of the body had to be connected directly to every other part, the body would consist of little but nerves. These exchanges, however, are very delicate and important things, and the gradual development and improvement of them have led finally to the human nervous system and the human brain, which are the most

(*a*) Some of the nerves of the human arm. The white strands are nerves: muscles and tendons also can be seen (p. 4). (*Rüdinger.*)



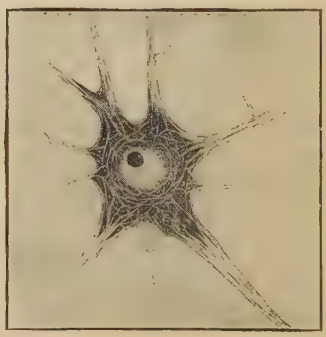
(*b*) Section across one of the bundles of the sciatic nerve of a dog (× 50). The little rings are the sheaths of the nerve-fibres (p. 5). (*Ranvier.*)



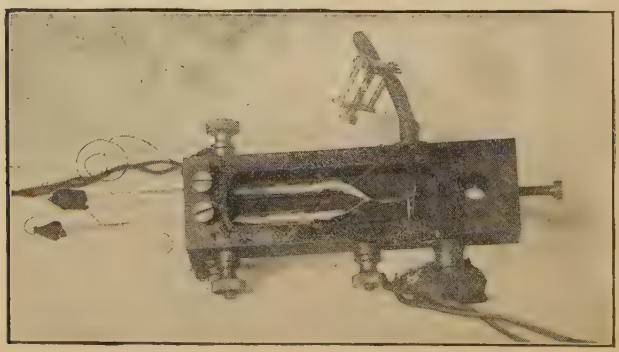
(*c*) Same as (*b*) but × 300 times (p. 5). (*Ranvier.*)

(*a*) The brain and spinal cord of a man (p. 9). (*Rudinger.*)

(*b*) Large cell of the human brain, highly magnified, with many nerve-fibres or processes running out of it to make connection with other cells elsewhere (p. 5). (*Schäfer.*)



(*c*) A motor nerve-cell from the spinal cord (p. 5).



(*d*) Chamber containing an isolated nerve—the white thread—to show the electric current produced either by an injury or by a stimulus (p. 5).

complicated, beautiful, and wonderful objects in the world. They are still largely automatic, like the automatic telephones, but they have come to possess, in the course of evolution, other faculties more complicated, more admirable, and more important than simple automatic action, namely, consciousness, intelligence, and freewill. All the same, however, they started as telephone exchanges, and it would be a bad day for us if they ceased to possess the power of doing most things automatically, without needing orders or asking advice.

I must return now to the messages which travel along the nerve-fibres themselves. These messages move very fast, not indeed as fast as wireless waves, which go 186,000 miles in a second, not even as fast as sound waves, which go 1,100 feet in a second. In human nerves they go about 400 feet per second, about 280 miles per hour. It is necessary that they should go fast: it is quite a long way from a man's

Speeds of Various Waves

Wireless and light	186,000 miles per second.
Sound in water	4,800 feet per second.
Sound in air	1,100 " "
Long waves (110 yards) on deep water	41 " "
Pulse wave in human arteries	18–36 " "
Ripples (2 inches) on water	1 foot "
Nerve Impulses—	
Man (37° C.)	400 feet "
Frog (18° C.)	95 " "
" (8° C.)	53 " "

toe up to his brain and back again. In the case of a very tall man it is about 4 yards, and if the message went only 2 yards a second (about the speed of a brisk walk) it would take such a man a second to think of taking his toe away when some one trod on it, and another second to do so. In the case of animals like giraffes, whales, and elephants, if the messages did not go very quickly along their nerves, it would occupy much too long a time for them to make the right response when anything awkward happened to them. In some animals, namely, cold-blooded animals, the nerve messages do travel more slowly, at a speed depending on the temperature: these animals, though, are generally small, so it does not matter very much: perhaps it may in the case of snakes and alligators. In a frog at room temperature the speed would be from 50 to 100 feet in a second. Everything goes on more quickly as an animal gets warmer. That is why tortoises run round so much more rapidly in the hot sun; that is why we keep our body temperature up (at considerable expense) so that we may move more quickly always. At our temperature, which is much higher than that of a frog, our nerve messages go four to eight times as fast as his.

It is not difficult to measure, at any rate roughly, how fast the messages go. Let us take the muscle-nerve preparation of a frog (fig. 1) and excite it at

two points, one a very long distance away from the muscle, and the other very close to it. The muscle responds earlier in the second case because the time taken by the message to run along the nerve is less. The difference of time can be measured (see fig. 3), and knowing the distance apart of the two points where we stimulate the nerve, we can calculate the speed of the message. We can do the same thing—though not very accurately—in man. We may apply an electric shock to one point of a man's body and measure how long he takes to do something in reply; then we may repeat the process with a shock at another point, and measure the time again. The time will be different by an amount depending on the distance between the two points; but the speed is so great that it is not easy to measure it in this way with any exactness. There are better ways of doing it.

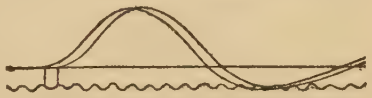


FIG. 3.—Record of two twitches of the same muscle caused by the same shock administered at two different points on the nerve, one nearer to and the other further from the muscle. The interval between the twitches is about $\frac{1}{100}$ second, which is the time taken for the impulse to travel between the two points. If the points were 10 cm. apart, the speed would be 15 metres per second. The vibrations shown on the bottom line were made by a tuning-fork oscillating 100 times a second.

The messages which travel along nerves are almost certainly of an electrical nature. They are not electric waves in the sense of wireless and light waves, since they do not travel nearly fast enough. There is a branch of chemistry known as "electro-chemistry," which deals with the electrical properties of

chemical things. The wave which travels in a nerve is a "wave of electro-chemical change"—that is, it is partly chemical and partly electrical. That there is a chemical side to its behaviour is now certain. A nerve requires oxygen; it breathes, just like any other living thing; and if it be more active it requires more oxygen to breathe. This oxygen is used in burning foodstuffs (protein, fat, or sugar) to supply energy. The waves which travel along a nerve require a certain amount of energy, as has lately been shown by a measurement of how much hotter they become when they are stimulated. The measurement is not easy. Even when a nerve carries 280 messages in a second, its temperature rises only $\frac{1}{14,000}$ part of a degree! A single message causes a rise of temperature of about a millionth of a degree. The amount of heat is very small, but it can be measured, and it is a sign (*a*) of chemical change taking place in the nerve as the message goes by, and (*b*) of chemical change taking place afterwards in "recovery" from activity.

The apparatus used in measuring the rise of temperature is illustrated by fig. 4. The nerve lies in the groove at the bottom, and is excited by the electrodes 1 and 2 at the top. The groove contains the "hot" junctions of 300 "thermo-couples," *i.e.* of elements made up by joining two different metals. When these junctions are heated an electric current

is set up, which is measured by an extremely sensitive galvanometer, reading to about one five hundred thousand millionth (2×10^{-12}) of an ampere. The

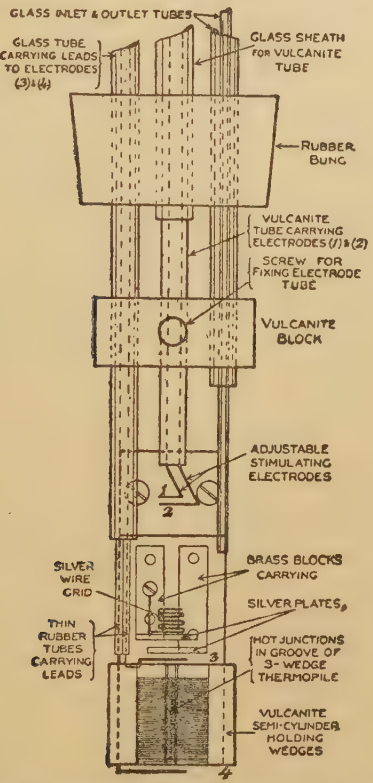


FIG. 4.—Apparatus used in measuring the rise of temperature of a nerve when stimulated.

apparatus is covered with a glass test-tube, and sunk in a large vacuum flask to keep its temperature constant.

That the message travelling through the nerve

has also an electrical side is shown by very many things, and has long been known. If we take a live nerve and cut or injure one end, then place it in a chamber such as that shown in Plate II, *d*, and connect an uninjured point and the injured end to a delicate electrical measuring instrument, we can show that an electric current runs in the nerve from the injured to the uninjured point. The same is true of many living things when injured. If we now

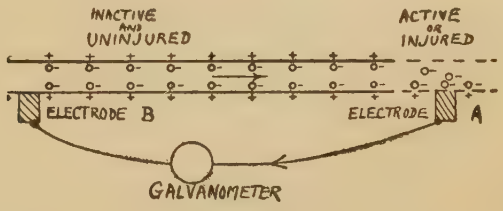


Fig. 5.

stimulate the nerve—that is, send messages along it—we find that each message is accompanied by a little electrical change which can be detected by the same instrument. Fig. 5 is a diagram of a nerve fibre connected by electrodes, A and B, to a galvanometer, G. The surface of the nerve is supposed to be in a state of "polarisation," positive ions (marked by ++) being outside, and negative ions (marked by O−) inside. These, owing to the attraction between positive and negative electricity, are trying to join each other, but cannot owing to the impermeability of the surface of the fibre. When

the nerve is injured, a path is made for them, and a stream of negative ions (shown by the arrow) passes along the inside of the nerve and reaches the electrode A, when the ions give up their electrons, which travel in the wire, through the galvanometer to the electrode B; there new ions are formed and join their partners on the outside of the fibre. During the passage of a message in an uninjured nerve the active point behaves momentarily just as though it had been injured, and allows the negative ions out to join their partners. In either case the electrons running through the wires of the galvanometer give a deflection which can be read. As the message passes along the nerve a little wave of electrical potential runs too. It is a very small wave, lasting only for a few thousandths of a second, but with the very delicate instruments now available, especially with the aid of amplifying valves (as used for radio), it is possible to record and measure this little electric wave, even when it occurs in only a single fibre (see Lecture V, fig. 40). Much of what we know about the behaviour of nerves, or at any rate of the messages which run along them, is due to studying the electric waves which accompany each message as it goes by.

The most beautiful way perhaps of showing and recording these waves is by means of an instrument called the "cathode ray oscillograph." In this in-

strument a stream of electrons [1]—that is, of minute particles of negative electricity—is shot out with high velocity, and the direction of the stream may either be recorded by allowing it to fall upon a photographic plate, or else made visible by putting a fluorescent screen in its path. This stream can be bent by electric or magnetic forces, and we use it to register the electric changes in the nerve. It is bent in one direction by the current produced by the nerve, and in another direction at right angles to the first by an arrangement connected with the stimulating circuit; and the instruments can be so arranged that so long as we go on stimulating the nerve the wave stands up still and clear in front of

[1] An atom of matter is supposed to be made up of negative particles of electricity circulating at high speed around a nucleus charged with positive electricity, the attraction between the two different kinds of electricity preventing the electrons from flying away. The current between the filament and the plate of an amplifying valve is carried by a cloud or stream of such electrons. Being charged with negative electricity, these particles are repelled by a negatively charged plate and attracted by a positively charged one. Moreover, a stream of such electrons is, in effect, an electric current, and we know that an electric current is attracted or repelled by a magnet or by another current. Thus a stream of electrons being shot out from a cathode may be attracted, or repelled, either by an electrically charged plate, or by an electric current, or by a magnet. When a current of electricity runs along a wire it is really due to a stream of these electrons jumping rapidly from one atom to the next of the metal of the wire.

us. We can study it, watch it, measure it up, photograph it, experiment with it as though it were a real objective stationary wave.

There are simpler ways in which the electric change accompanying a nerve passage can be demonstrated. We have only to take a nerve and connect it by its middle and by one cut end to a sensitive

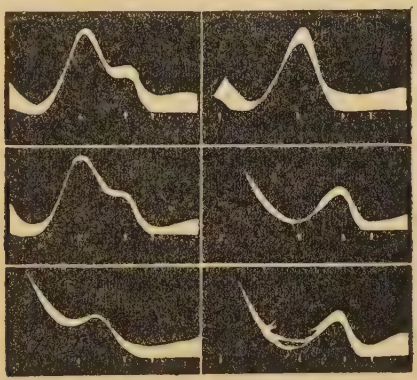


FIG. 6.—The electric change which travels in a nerve recorded as a standing wave by the "cathode ray oscillograph." A photographic plate is exposed to the wave as it stands on the screen and the record is made. Six separate waves are shown recorded under different conditions (Erlanger & Gasser).

galvanometer, and we get a movement at once when we stimulate the nerve. Galvanometers are instruments for detecting and measuring electric currents (see Plate III, *a*), and they can be made almost incredibly sensitive. The current which runs through an electric lamp may be about 1 ampere: it is not impossible to-day to adjust a sensitive galvanometer so that it would give a movement of about half a million miles for such a current—in other words,

it will read to a million-millionth of an ampere. Such sensitive instruments are not necessary except for special purposes, though there are some experiments (for example, those on the heat production of nerve, referred to above) which require all the sensitivity one can get.

This last method does not record the individual waves that travel along the nerve; it simply, so to speak, adds them all up and gives us an answer on the scale. To show the single individual wave we may use another kind of instrument (the "string-galvanometer" or the "capillary electrometer"), which I will describe in a later lecture. The galvanometer, however, was the first means of measuring the electric change in nerve, and it is still one of the simplest and best.

It is interesting to recall that Galvani, a Professor of Anatomy at Bologna, whose experiments on frog's muscles first drew attention to the existence of current electricity, was also the first to demonstrate the existence of animal electricity.[1] A nerve-

[1] It has often been stated that, in 1776, Galvani had skinned some frogs to make broth for his wife, who was in delicate health: that the leg of one of these, on being accidentally touched by a knife which had lain near an electrical machine, was thrown into violent twitchings: and that thus his attention was directed to the relations of animal function to electricity. In fact, however, fifteen years earlier he was engaged in experiments as to the action of electricity on the muscles of frogs. His discoveries

muscle preparation is laid upon a glass plate (fig. 7), the nerve is raised upon a glass rod, and its freshly cut end is allowed to drop and touch the muscle. A contraction occurs, which is due to the stimulation

FIG. 7.—Galvani's experiment to demonstrate the existence of animal electric currents (Waller, *Human Physiology*).

of the nerve by means of its own "injury current." A nerve may be stimulated also by the "action current" of a muscle which is itself undergoing a stimulus. Fig. 8 shows how the "action current"

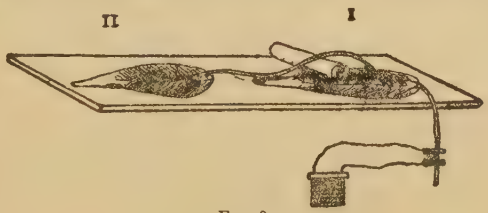


FIG. 8.

of one muscle, when its nerve is stimulated, excites the nerve of a second muscle, causing it, too, to contract. The nerve on the right is stimulated by the coil. The right-hand muscle contracts; a wave of electrical potential travels along it, exciting the

really started from the observation that the suspension of frogs' legs on an iron railing by copper hooks caused twitchings, which we should now describe as being due to the galvanic current (so called after him) produced by two different metals in contact with the same substance containing salt in solution.

nerve of the left-hand muscle, which also contracts. This experiment, which is an easy and convincing one to make, shows clearly, with the simplest apparatus, that muscles produce electric currents when they are excited.

Other parts of the body show the same kind of electric change: for example, the heart, the muscles, and even the glands and the retina of the eye. Fig. 9 is a record demonstrating the production of electric

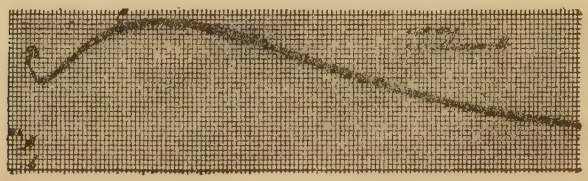


FIG. 9.—Record of electric currents produced by the retina of the eye (Einthoven).

currents by the retina of the eye. The eye has been accommodated for darkness, and at the beginning of the record light is allowed to fall on the retina for $\frac{1}{100}$ second. There is an immediate response and the complicated curve traced out is supposed to correspond to three different substances in the retina, A, B, and C. The horizontal divisions are $\frac{1}{2}$ second, the vertical divisions are $\frac{1}{100,000}$ volt. The whole response therefore amounts only to about $\frac{1}{4,000}$ volt, which shows what sensitive instruments are required for such purposes.

Some fishes (*e.g.* gymnotus, torpedo, and malapterurus) have electric organs which are powerful

batteries, from which a succession of rapid electric shocks can be liberated at will by the fish, paralysing or stunning his enemy or prey. Plate III, *b* shows a Japanese electric ray and its electric organ. The adult fish is about a foot long measured from head to tail. The electric organ consists of a pair of large flat bodies, one on either side. Each of these is an assemblage of vertical six-sided columns, about 200 in number, and half an inch high. Each column consists of about 400 disc-like "electric plates" composed of a jelly-like material. From the electric lobe of the brain five "electric nerves" run to each half of the organ, branching until one nerve-fibre enters each disc on its ventral side. When the organ discharges electricity—which happens when a message comes to it along its nerves—the side of the plate just mentioned becomes negative, the back side positive. The discharge is of the order of 30 volts, which in sea-water gives a nasty shock. Assuming that the columns are electrically "in parallel" and the discs "in series," each disc on stimulation by its nerve must develop about 75 millivolts. The electric discharge can be recorded by an "oscillograph" such as engineers use on the electric power mains.

Fig. 10 shows the discharge of the electric organ after complete rmeoval from the body of the fish. The organ is held between two large metal plates pressing on its front and back surfaces, and directly

stimulated by an electric shock. The first rise of the curve shows the stimulating current, the second the response of the electric organ to the stimulus, and the third the response of the organ to the shock of its own current. The electric organ would well repay further investigation. At present, however, we know more about the electric change in nerve than in anything else, because nerves are so much

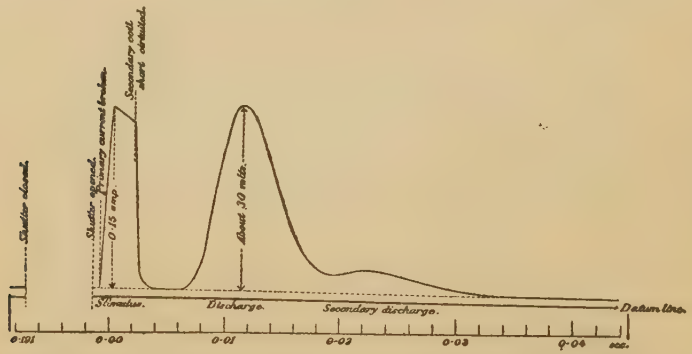


FIG. 10.—Discharge of the isolated electric organ of the Japanese ray (Fuji).

simpler in nature and in structure, and so much easier to obtain and to experiment with.

I have several times spoken about "stimulating" a nerve. A nerve can be stimulated in various ways, apart from the natural ways that exist in the body: we can tap it, warm it, put chemical substances on it; but all these things are apt to injure it, too, and much the best way is to employ an electric shock.

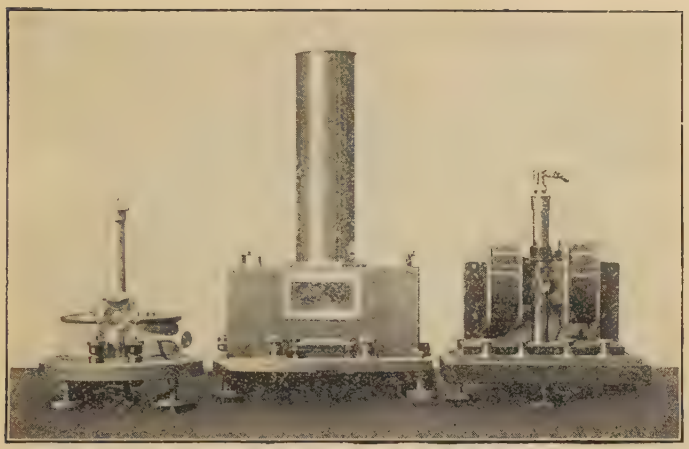
Electric shocks have, in fact, been used for many years for the purpose. In a book by Francis Hauks-

bee, F.R.S.,[1] published in London in 1709, it is stated: "The *Nature* and *Laws* of *Electrical Attractions* "have not yet been considered by any: and in the "following observations, 'tis hoped, the Reader may "meet with many things which may be of great use in "discovering some of the wonderful and hitherto un- "heeded Effects of the stranger Properties of Bodies, "in several of the Operations of Nature: and possibly "in the Production and Determination even of *In-* "*voluntary Motions* in the *Parts of Animals;* of which "very little has yet been written intelligibly." How truly Hauksbee predicted the usefulness of electricity in discovering wonderful and unheeded effects, both in the non-living and the living world, and how pleased he would be to-day to witness the involuntary motions in the parts of animals (and men) which we can now produce, and exhibit, by such means; though it may still be true that very little that is written on the subject is intelligible!

We may stimulate a nerve for hours, provided that we give it oxygen, and it will be going almost as well in the end as it was at the beginning; which is due to the fact that it uses so very little energy. It may be shown that a nerve stimulated 250 times a second for 10 hours will require, as fuel to carry 9,000,000 messages, only $\frac{1}{2000}$ of its weight of sugar.

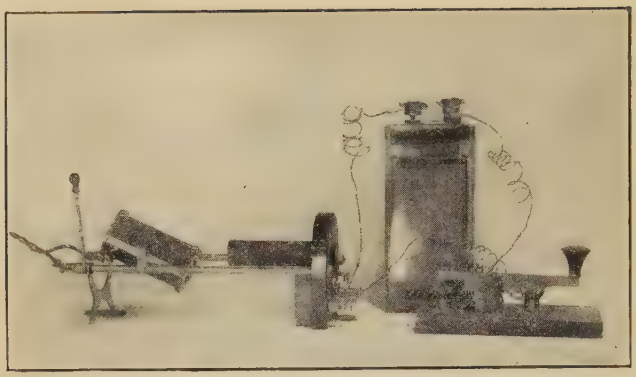
[1] My thanks are due to Professor Andrade for calling my attention to this passage and prediction.

We can stimulate a nerve with an induction shock from a coil, with a discharge from a condenser, and either by a constant current or by an alternating one. In a "constant" current the electrons always move in the same direction in the wires; in the "alternating" or "oscillating" current they run first one way and then the other, their movements being constantly reversed. A constant current passed through a telephone makes a single click; an alternating current makes a continuous hum. Some of our houses have direct current, others alternating current. In our wireless aerials the current is an oscillating one; in our electric bells it is direct. A constant current passed through a nerve excites it only twice—once when the current begins, once when it ends. An alternating current, provided that it does not alternate too rapidly, stimulates it twice for every oscillation. The usual way of stimulating a nerve is by an induction coil (Plate IV, *a*), by means of which we can put a single sudden burst of current into the nerve and so excite it once. In this instrument the making or breaking of a current in the primary coil causes a rapid induction "shock," *i.e.* a sudden burst of current, in the secondary coil. This is one of the best and simplest forms of electric stimulus. Keeping the primary current constant the shock can be varied by altering the position of the secondary coil, *i.e.* by moving it backwards or

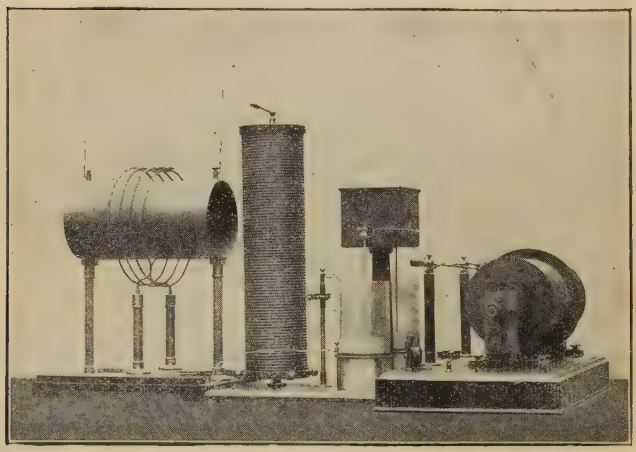


(*a*) Three galvanometers. The middle one very slow and sensitive, the one on right very quick but insensitive, the one on left sensitive and fairly quick. Their movements can be amplified many times by means of a "thermal relay," as is done in measuring nerve heat (p. 19).

(*b*) Japanese electric ray showing the electric organ (A, A), the electric lobe of the brain (B), and the electric nerves (C, C) (p. 24). (*Fuji.*)



(*a*) An induction coil as used for physiological purposes with accumulator and key (p. 26).



(*b*) Tesla coil supplying an alternating current of high frequency (*e.g.* a million oscillations a second). This current is quite without effect on an animal or man in spite of its enormous voltage (p. 28).

forwards, or by tilting it up. If a *sequence* of shocks be required the battery is joined to two special terminals, which allow the current to be made and broken automatically as in an electric bell. When the coil is made to buzz the nerve is excited for each movement of the buzzer.

Such experiments can be made on human subjects. The ulnar nerve of the arm, running just beneath the electrode shown in Plate VII, is a very suitable nerve to study. It is not very deep—near the elbow it is very close to the surface, as you find if you bang your "funny-bone,"—and it is very easily stimulated. It supplies some of the muscles of the forearm and of the hand, and of these perhaps the easiest to observe is the one which bends the little finger. We bring the current into the body by means of a large, flat, damp electrode placed in some neutral position: for example, the calf of the leg. The current is very diffuse owing to the size of the electrode, and there is no nerve near the surface on which the large electrode lies, consequently there is no effect at all at the electrode on the calf. The current is taken out of the body by a small damp electrode held on the end of a rod, and the stimulus occurs at the point where the current leaves the body. If we put a constant current into the ulnar nerve of a man's arm we can see his little finger twitch when the current is turned on, but nothing happens all the

rest of the time while it is running. He behaves like a telephone, which gives a "click" when the current begins, but nothing while it continues to pass. If we put a condenser discharge, or an induction shock into him, again we see a single twitch of his finger. If we employ a series of condenser discharges, or an alternating current, then his finger shows a rapid series of twitches, one to each discharge or alternation, which can be caused to merge into one another by making their frequency sufficiently high. As we increase the frequency the contraction becomes stronger and more continuous, until, at last, at very high frequencies we come to a most astonishing thing; its explanation gives an important clue as to the means by which an electric current produces its stimulating effect. If we take a really "high frequency" current, such as we pick up in our wireless aerials—we may make it by means of a valve-generator of some kind, or of a Tesla coil (Plate IV, *b*),—then it has no effect whatever. We may touch the wires, we may draw off long sparks from them, and we feel nothing whatever except a little prick due to the heat generated by the current at the point where it enters the skin. We may employ 100,000 or 1,000,000 volts, and a child may play with the wires without danger, provided that the frequency is sufficiently high. If it is low (like that in alternating current power mains) a hundredth or

a thousandth of the voltage will cause instant death. We may place an animal inside a coil carrying a current of high frequency, and warm him up, without injury, by currents induced in his conducting tissues. We might even warm ourselves, in our houses, without warming the latter, by winding our rooms with wires carrying high frequency currents! Though in that case we should not be able to carry metallic

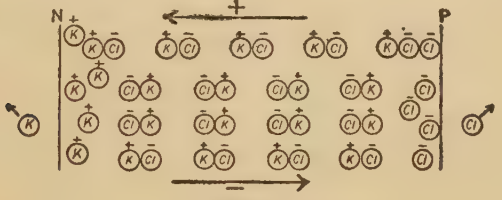


FIG. 11.

money, which might burn holes in our pockets. How can we explain the absence of stimulating effect?

To understand the matter, properly we must learn something about the way in which an electric current stimulates a nerve; and to understand that we must know a little of what happens when an electric current runs through a wet substance such as all living things are. From the electrical point of view living material is much the same as a solution of salt, with a large number of partitions erected inside it. In fig. 11 we have a solution in water of potassium chloride, KCl, the potassium, K, being positively charged (having lost a negative electron), and the chlorine, Cl, negatively charged (having gained an

electron). When a current runs from P to N in the solution the positive ions (potassium) go in the direction of the arrow marked +, while the negative ions (chlorine) go in the direction of the arrow marked —. Supposing P and N to be membranes which stop the ions from passing, the positive ions will bank up at N, while the negative ions will bank up at P. This happens in muscles and nerves, and when the banking up has gone far enough something collapses, the bank of ions break down and a "stimulus" occurs.

Three-quarters of the body is water and an important part of the rest is salt, and when we dissolve salt in water a current will run through the water, which is otherwise a non-conductor. When an electric current runs through a wire it is really carried by a stream of electrons—minute particles of negative electricity—running along the wire; but when an electric current passes through water containing salt it does not travel in this way, but by the movement of what are called "ions," actual particles of matter, sodium, chlorine, or whatever it may be, which carry electric charges. If, then, we put an electric current through water we find that some of the substances, those with the positive electricity (such as sodium or potassium), tend to travel towards the negative pole N and collect there, while other substances, those carrying a negative charge (such

as chlorine), move towards the positive pole P and collect there. It is very easy to show this when the substances in question are coloured; then when we turn the current on we can see the coloured materials travelling towards one pole or the other. Fig. 12 shows this clearly. The lower portion of the tube contains copper sulphate solution ($CuSO_4$) in gela-

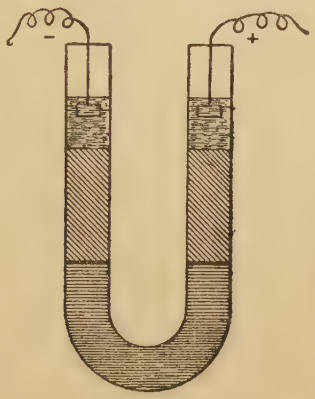


Fig. 12.—Movement of coloured ions when a current passes.

tine, the middle portion some colourless salt in gelatine, the top portion the colourless salt only. The copper ions are blue, and when a current passes from right to left the blue solution passes over gradually in the same direction. To mark the original position some charcoal is scattered on the surface of the copper sulphate jelly; this is left behind, while the copper moves over. The sulphate ions travel to the right, but they are colourless and cannot be seen; if, however, we put a little barium salt into the

colourless solution on the right a cloudy precipitate will appear, due to the formation of barium sulphate.

Now living material is like a salt solution filled with partitions of all kinds. These partitions may be the boundaries, the outside walls of the cells, or they may be membranes passing across the cells inside. Anyhow, they stop the free movement of the substances dissolved in the water, so that when an electric current is passed through, these substances tend to "bank up" at the partitions; and when they have banked up enough, when, in fact, the tissue—in electrical terms—has become sufficiently "polarised," something collapses and the stimulus occurs. Whenever, therefore, an animal or a nerve is stimulated by an electric shock, you must think of the current as having piled up a bank of chemical substances at some partition within the tissue, and when the bank is high enough something gives way and the message goes off.

Now it will be easy to understand why a current oscillating rapidly enough will not excite. An oscillating current consists of electricity running first one way and then the other. First of all it carries the chemical substances in one direction and *tends* to bank them up at one membrane. But if it oscillates fast enough, before it has done anything very much in this direction, it has started running in the

opposite direction and begun to undo all that it did before. We can show the same thing with the coloured solution (fig. 12). The colour moves when we turn a constant current on, but it stays quite still when we use an alternating current, however strong. If an oscillating current is to produce an effect, its oscillations must not be so rapid that the effect of the current in one direction is completely undone by the following current in the opposite direction. That is all there is to it. That is why a constant current of one or two volts can easily be felt when the hands are wet, and why thousands or even millions of volts are quite without effect when the current alternates sufficiently rapidly. The oscillations, however, must be very rapid indeed, as they are with a Tesla coil; otherwise each current has time to produce its effect before it is neutralised by a current running in the opposite direction, and the alternating current may then be just as unpleasant and dangerous as a constant one.

We have discussed so far the way in which a nerve works, and the chief object of these lectures is to explain, so far as is possible at present, the way in which the parts of the body *work*. There is another side, however, to the activities of the body, an equally important side, that relating to the *growth* as distinguished from the *working* of it. With growth itself I do not propose to deal, but there is

one aspect of the matter—regeneration and recovery from injury, which are fundamentally the same thing as growth—about which I should like to say a few words in connection with nerve. If a nerve be injured or cut, either by accident or in an experiment, the part of it which is separated from the nerve-cell to which it belongs degenerates and dies and disappears. If we simply divide a nerve and separate the two cut ends, then the lower half dies, being separated from its nerve-cell, while the upper half remains alive. What the influence of the nerve-cell is upon the fibre we have very little idea. Why a nerve which may be yards long in a large animal should remain alive for many years, provided that it is in connection with its nerve-cell, yet dies at once if the nerve-cell is cut away from it, we do not know. It is a very astonishing thing that a nerve-cell, a minute object only a few hundredths of a millimetre across, in the spinal cord (say) of a whale or elephant, can exert a continuous influence on a strand of nerve-fibre connected with it many yards away. The nerve-fibre may be 5 metres or more long and only a few thousandths of a millimetre across; it may, in fact, be a million times as long as it is thick, like a telephone wire joining a house to the exchange; and yet some influence is being transmitted along it continuously, which is necessary for its continual maintenance in health and activity,

and as soon as that influence is cut off by section of the nerve the fibre dies. As Sir William Hardy once pointed out in a lecture to the Chemical Society, it would take almost geological time for any actual substance to be transmitted by diffusion along such a nerve-fibre from the cell to which it belongs: and anything diffusing down would certainly get lost before it reached the end. It must presumably be something different from that, something which (for want of a better name) I have called an "influence." Either the passage of nerve messages along a fibre is necessary for its continued health, or else there is some organisation of its molecules, something analogous to the structure of a crystalline liquid transmitted from molecule to molecule along the nerve, which collapses as soon as the fibre is cut off from the influence of a similar organisation in the parts lying near to it. Anyhow, the fact of this influence of the nerve-cell on the nerve-fibre remains, and it is one of the most entrancing mysteries in biology.

When a nerve has been cut, the lower part dies but the upper part lives, and if the upper part be given a chance it will grow down again along its old track bit by bit, until all its old function is, restored. It is usually necessary that the two ends of the cut nerves should be brought close together, so that the fibres may grow down along their old

track and find their way to the organ (muscle, or sensitive end-organ, or gland) to which they were originally connected: in some cases, as in that of the nerves to the heart, no juxtaposition is necessary, and the fibres can find their way unaided. It is amazing that they are able to find their way. When a nerve regenerates, its function comes back just as it was before. The fibres which ran to muscles, bringing them messages—that is, orders to contract, —do not now by any chance run off to sensory end-organs in the skin, nor do sensory nerves grow down and attempt to join on to muscle-fibres. In some mysterious way each nerve-fibre seems to know where it has to go, and after a long interval the function is restored.

Such experiments have been performed many times on men, not only as the result of accident, but sometimes intentionally in the laboratory. For example, Head and Rivers record (*Brain*, 1908) a human experiment in nerve division, in which a sensory nerve in one of their arms was cut and allowed to die and then to regenerate, and the sensations occurring in the affected portions were studied during the process. Nerves may even be crossed. If two nerves, A and B, lying near to one another in the body, be both cut, and the upper end of A brought and sutured to the lower end of B, and *vice versa*, then A will grow down to the muscles originally

supplied by B, and B down to the muscles originally supplied by A. This method has been used on human patients affected by paralysis of a group of muscles, owing to imperfect functioning of the nerves leading down to it. By such means paralysis of the face has been practically cured, the process of governing the muscles of the face being taken on by a nerve which previously brought orders to much less important muscles in the shoulder.

Let us now return to the question of how a nerve works. One of the best ways of understanding a thing is to try to make a model of it. The model we will discuss is a chemical, or perhaps it would be better to call it a physico-chemical, one. You will remember that earlier I said that the nervous impulse is a wave of electro-chemical change passing along the fibres. In the model to be described you can see the waves passing, you can recognise the chemical changes which occur, and you can measure the current which takes part. R. S. Lillie has drawn attention to the great likeness that exists between the impulse which travels in a nerve and the one that travels in the model. The likeness applies not only to the more obvious characteristics of both, but to the finer and more subtle features; and if we want to obtain a picture of what happens in a live nerve when a message travels along it, we cannot do better than try to understand the action of the

model. A model is not everything: the nerve does not behave in quite the same way as an iron wire standing in nitric acid. Do not imagine that we have explained things when we have made a model of them. Maybe the real thing is very different. Nevertheless, a model, taken with a suitable grain of salt, may prove a very valuable appetiser before trying to digest the real article.

If an iron wire be immersed in nitric acid of sufficient strength (specific gravity exceeding 1.2) it reacts only momentarily with the acid, and then enters into a passive state in which no further solution occurs. A thin film of oxide, or of some passive material, is developed on its surface and maintained by further reaction if it happens to be broken, so keeping the iron and the nitric acid apart. Yet this seemingly stable system is highly reactive. If we pass an electric current through a short length of it, or touch one end with a bit of zinc, a sudden change will start off and be propagated as a wave from the point "stimulated," or touched by the zinc, until the whole length of the wire has been "excited." The wire turns black, bubbles of gas come off, and in a few moments it resumes its former passive state. Thus the iron wire transmits a "self-propagating electro-chemical change," limited to its surface film, capable of being started by a variety of means, chemical, electrical, mechanical, and even able to

jump from one wire to another which is immediately in contact with it.

The means by which this wave is propagated in iron wire is not completely understood, but is almost certainly electrical in nature. The film which exists on the surface and which keeps the iron and the nitric acid apart can be altered, or removed, or rendered porous, by passing an electric current through it.

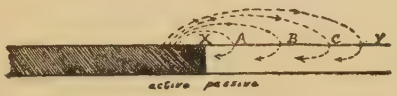


Fig. 13.—Iron wire in nitric acid (R. S. Lillie).

In fig. 13 an iron wire is shown in nitric acid (60 volumes per cent. of commercial HNO_3, sp. gr. 1.42). A passive film is formed on the surface, keeping iron and acid apart. Then, if the film be locally removed (as on the left—region shaded black), the iron reacts with the acid, producing a current as shown by the arrows, which clears the film off the neighbouring region (on the right) and so causes it also to become active. This area in turn affects the wire still further on, and thus "a wave of electrochemical change" is propagated. We know if we put two different metals into a salt solution that we can draw a current from them. This is Galvani's original experiment, and all who have worked with electricity have used galvanic batteries. Now, when

a portion of the iron wire had been cleared, by means of the stimulus, of its passive film, we have two different substances in contact with the nitric acid, namely, iron on the left (fig. 13) and film on the right. These act as though they were different metals and a current tends to pass from one to the other in the solution, as shown by the arrows in the figure, returning to complete the circuit through the wire itself. This current alters or removes the film on the right-hand portion of the wire, which then is free to react with the acid, so that now the same thing goes on again between this portion and the part further to the right. This in its turn gets cleared of film, reacts with the acid, and produces the same effect still further on. Thus a wave is propagated, the film is cleared off the whole surface of the wire, which reacts for a short time with the acid and then forms its film over again.

You can picture just such a process happening in all the nerve-fibres of the body whenever messages are started off in them. We do not understand the matter yet, but some day we shall. There is nothing essentially mysterious in it: with the help of physics and chemistry we ought to be able to understand it, though probably physicists and chemists will have to discover much more before we can; and when we do understand it, we shall find (as people have found with X-rays and radio and countless other

things) that there are all kinds of ways in which we shall be able to use the knowledge we have gained.

Note.—The experiment described is perfectly simple to make and is very instructive. For further information, see the papers by R. S. Lillie in the *American Journal of Physiology*, *Science*, *Journal of Physical Chemistry*, and *Journal of General Physiology*; or his book, *Protoplasmic Action and Nervous Action* (University of Chicago Press), p. 253, etc.

LECTURE II

Muscles and how they Move

All our movements are carried out by means of muscles. Muscles are of various kinds, which come into three chief classes: (1) Those called *voluntary*, which respond rapidly to the will, which move our limbs when we order them to (see Plate V, *a*), or hold them fast if we desire. (2) Those called *involuntary*, which we cannot control directly by the will; which work our vital organs, such as our digestive apparatus; which surround our blood-vessels and adjust our blood pressure; which manage what we may call the "domestic arrangements" of our bodies, and do various odd jobs about the house without our constant supervision, often without our knowledge: they usually move slowly. (3) The *heart muscle*, which in many ways lies somewhere between the other two great classes, which also we cannot regulate by our will, but which responds very quickly to our needs and activities. The heart muscle is concerned with one job only—it is a pump circulating blood around the body. In this lecture I propose to discuss only the first class of muscles, those which are directly under our control, which deal with our external rather than our domestic activities.

In order to understand a muscle, as to understand any living thing or organ, one must first take a microscope and see what are the elementary units of which it is made up. All animals and organs are communities of living cells, and the properties of the material of which they are composed and of the world in which they exist are such that these living units must of necessity be small. We cannot imagine a motor-car as big as the *Aquitania* and in other respects like an ordinary motor-car: the nature of the materials of which it has to be made is such that it would not work. Neither can we imagine the *Aquitania* reduced to the size of a watch but otherwise similar in all its parts: the properties of water and air, as well as of its materials, are such that again it would not work. So also with the units of which animals are made up. They have to be about of a certain size or they refuse to function properly, and the particular size they must attain, and may not exceed, is one which our unaided eyes do not allow us to perceive. We have, in fact, to use a microscope to see the units of which a muscle is composed. The muscle as we know it, the red meat, consists of thousands of muscle fibres, each working in the same way, each obeying the orders of its owner, all working together as members of a well-organised community for the good of the whole.

A muscle fibre is a long, thin, jelly-like thread

(Plate V, *b*) about $\frac{1}{500}$ of an inch in diameter, and, in the case of voluntary muscle, marked with what are called cross-striations at regular intervals across it. It lies inside a thin transparent covering (the "Sarcolemma") which ends in the tendon by which it is connected to the bone, or other object, which it moves. What the cross-striations are nobody knows, nor why they are generally, but not always, more vivid in the muscles which are able to move more rapidly. These muscle-fibres, thousands of them, lie side by side in bundles forming the mass of muscle which we can see and feel. Each fibre (see Plate V, *c*) consists of a large number of fibrils lying in a semi-fluid medium, the "sarcoplasm," and bound together by the "sarcolemma" which surrounds the fibre. The fibrils are probably the actual units of the contractile machine. The mass of fibres is intersected in all directions by a maze of blood-vessels, which supply each individual fibre with the food and oxygen which it requires. The roads which intersect the country are always carrying a certain amount of traffic; and at times, when the need is great, when supplies are urgently required, when "something is doing" in a particular neighbourhood, they are crowded with traffic right up to their full capacity. So it is with the muscle. There are innumerable roads, namely, the blood-vessels, arteries, capillaries, and veins, which intersect the

tissue in every direction; usually most of these are closed, but when the need is great, they open up wider and allow a much greater traffic to go by. When we are at rest the blood flow through our muscles is small; when we are active and they need more oxygen and food, the blood-vessels open up, the blood goes rushing through, and the needs of the individual fibres are met.

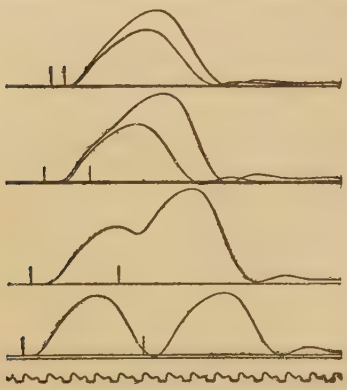


FIG. 14.—Record of two twitches of the same muscle, with different intervals between them. In the lowest record the interval is so long that the twitches are separate; as we pass upwards the interval is diminished and the twitches tend to fuse; in the highest the fusion is so complete that the result looks like a single larger twitch. For comparison, in the upper two records, a single twitch is given, in addition to the fused pair. The vertical lines show the moments of stimulation. The line at the bottom gives time marks —50 per second (Pembrey).

Each muscle-fibre has a nerve-fibre coming down to it, along which it receives the messages ordering it to work. These nerve-fibres join their muscle-fibres at the motor nerve-endings. Plate VI, *a* shows a somewhat fanciful drawing of a motor end organ.

Plate VI, *b* is an actual micro-photograph of muscle-fibres. There is a pathetic interest attached to this picture. It was made in London, shortly before his death in a lift-shaft accident on his sixty-ninth birthday, by Professor Kulchitsky, who at one time was Professor of Histology at Kharkov. After retiring from his

Chair he interested himself in Public Education in Russia, and in 1916 became Imperial Minister of Education. After the Russian Revolution he escaped to England, and worked for nearly three years at University College, London; there he spent much of his time in making these beautiful preparations of nerve-endings in muscle. At these nerve-endings the messages pass over from the nerve-fibres to the muscle-fibres and cause the latter to respond.

When a muscle-fibre gets a single message along its nerve it gives a single twitch, when it gets two messages it gives two twitches; by connecting it to a lever it can be made to write these twitches on the smoked surface of a moving drum (see fig. 14). If the second message comes sufficiently close on the first one's heels, the twitches fuse together and give one larger and more prolonged twitch. If messages come in rapid sequence (see fig. 15) the twitches may all join up to form one apparently continuous contraction.

It is easy to try this experiment on human subjects. In Plate VII is shown a boy applying a stimulus to the ulnar nerve of his arm. The other electrode is a large flat plate, pressing on the calf of his leg. The stimulating agent is a condenser discharge, of which the cathode is the electrode seen in his left hand. The machine [1] shown in the fore-

[1] Made by Messrs Watson & Sons (Electro-medical) Ltd. of London.

ground can provide condenser discharges of any strength, and at any frequency desired. His little finger, which is worked by muscles supplied by the ulnar nerve, is connected by a string to a little spring, held in a clamp and provided with a reflecting

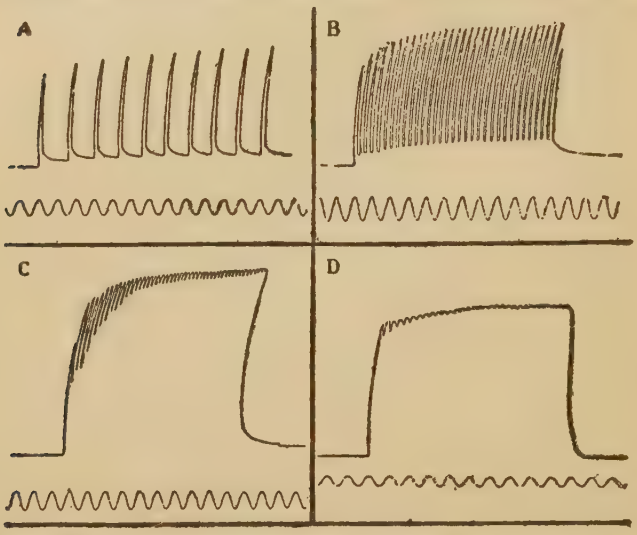


FIG. 15.—Fusion of twitches to form a prolonged contraction. A, twitches so infrequent that there is practically no fusion; B, C, D, with increasing frequency and increasing fusion. Time tracing at the bottom in half-seconds (Halliburton).

mirror. When his finger twitches the spring is bent and the mirror is twisted round. A beam of light from a lamp shines on the mirror, which reflects it back on to a screen, so that the movements of the finger can be demonstrated by the oscillations of the spot of light on the screen. If the condenser discharges come at sufficient intervals the spot of light just moves up and down between two fixed

positions, once up and once down for each twitch of the muscles. If the intervals be diminished, *i.e.* the frequency of stimulation increased, the spot of light does not return to its original position after each twitch, but remains up. There is a partial fusion of the twitches. If the frequency be made greater and greater, the fusion becomes more and more complete, until finally the contraction appears to be perfectly smooth and continuous. The experiment is a beautiful and simple one to make. It is being made in Plate VII by a boy only 11½ years old.

Let me emphasise again the nature of a muscle twitch. A twitch is the elementary unit of which all muscular contraction is built up, and it is necessary to understand its nature. A twitch is not the same thing as a contraction. A twitch consists of three separate phases: a first phase, the development of a force or the lifting of a load; a second phase, the disappearance of the force—the lowering of the load; and a third phase, recovery. Just as matter is made up of atoms, sound of waves, electricity of electrons, so muscular contraction is made up of a series of twitches of the individual elements of the muscle, fused together in the appropriate way. In Nature, however, a muscle twitch is a very rare thing, though easy enough to produce in a laboratory. In ordinary life our movements do not consist of

twitches; these are much too sudden, and end too quickly to be much use for our usual movements. In ordinary life we work by means of prolonged contractions, which are made up of large numbers of twitches fused together, as shown in fig. 15 and in the above experiment. That this is so is proved by the record given in fig. 16, which is a tracing on moving photographic paper of the electric currents produced by the muscles of a man's arm during contraction, the individual oscillations corresponding

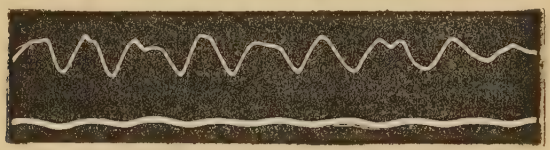


FIG. 16.—Record of oscillations produced by voluntary contraction of arm muscle when connected to a string galvanometer. One electrode, moistened with salt water is placed on the skin directly over the active muscle, while another is placed at an inactive point. The main waves occur about 50 times a second. The lower curve is a time marker going exactly 50 times a second (Piper).

to the individual twitches of which the contraction is composed. When a muscle gives a single twitch a single electric wave travels along it; when it gives a hundred twitches, whether fused together or not, a hundred electric waves travel along. These waves can be recorded by the string galvanometer shown in Plate XI, *b*. An electrode, moistened with salt water, is placed on the skin directly over the active muscle, while another is placed at an inactive point. At first, before the muscle contracts, the galvanometer stands still. On the word "go" the subject

contracts his muscle, *e.g.* the biceps of his arm, and the galvanometer immediately begins to oscillate, 50 times a second or more, much too fast to count, but not too fast to record on a moving photographic plate. Similar records of the electric currents pro-

Fig. 17.

duced by a contracting muscle can be made on other animals. Fig. 17 shows such an experiment on an elephant. In 1919 two elephants were awaiting their turn to be exhibited to the patients in the Children's Hospital at the Harvard Medical School. While they waited records were taken upon the contracting muscles of their trunks in the manner shown in the figure. The animal itself gripped the lower electrode, while the upper electrode was pressed against its forehead. A record so obtained was exactly similar to that found in the case of man. The frequency of the main waves was about 48 per

second, which agrees closely with that commonly found in the muscles of the human arm.

We cannot make our muscles give single twitches by natural means. If one asked the boy shown in Plate VII to move his finger as rapidly as he possibly could, the result was never more than about eight movements a second of the spot of light; whereas twitches can follow each other very much faster than this without fusing completely together. If we analyse what happens, even in the shortest voluntary movement, we find a volley of impulses fired down the nerve in rapid succession, and half a dozen or more twitches fused together in the muscle.

When a muscle contracts, it shortens—if it be allowed—and so does work, pulling upon the bone to which it is attached. If it be not allowed to shorten, it merely goes hard and stiff, it exerts a force without doing work, and maintains the limb and body in position. When we wish to hold a limb rigid we do so by opposing one muscle to another, the two pulling in opposite directions. When a muscle is stimulated it will shorten if it can, and the only way to stop it is to oppose it either by something too heavy or too strong to move, or else by the contraction of an antagonist muscle.

For a hundred years or more one of the chief occupations of physiologists has been the study of

muscle. There are several reasons for this: one is its obvious importance, since almost half the weight of the body consists of muscle, and all our external activities are carried out by its means. Another reason is that it shows effects which can be measured —work, heat, and electricity—by accurate physical means, and people have long realised that advance in science comes most quickly from accurate quantitative measurements. A third reason is that in muscle nature has provided us with an extremely convenient thing to study. If we kill an animal and take its liver out, we find it extremely difficult to discover what the liver is—or was—doing, indeed to see that it is doing anything at all. It is possible, but it requires much apparatus and great skill, to take out a kidney from an animal and to persuade it to function for a while after removal. With a muscle, however, it is so easy that anyone can do it. We have only to kill a frog and cut out a muscle, and it is difficult to do it so clumsily that the muscle will not work for hours afterwards. If a muscle be carefully prepared and kept in salt water containing the appropriate salts, and protected from the invasion of bacteria, it may live and continue to function not merely for days but for weeks after removal from its previous owner. Most of what we know about muscle started from experiments made in this way upon muscles isolated from the body and

examined under appropriate conditions. Of course these conditions are unnaturally simple, and in the body the behaviour of muscles is more complex: we have to examine them also in living animals, and especially in man, in order properly to understand them. It is true, nevertheless, that little knowledge could have come if we had not started with isolated muscles, and then led up gradually to the more complicated problem of muscles at work in their natural home, amid the environment of the body as a whole. In this Lecture I shall tell you particularly about muscles in their simplest form, isolated from the body of their owner.

Muscles consist of bundles of contractile fibres, held together by what is called connective tissue, and running at their two ends into tendons, the tendons of all the fibres being joined together to form the tendon of the main muscle. The "origin" of a muscle is the fixed point at which the muscle is attached to a bone. The "insertion" of a muscle is the point at which it joins the part that is moved. In the case of some muscles the tendons are quite short, and the fibres themselves seem to end practically on the bone. In other cases the tendons are very long, as in that of the muscles which work the hand. The muscles that move the hand and the fingers are largely in the forearm, and, since they have to do their work a long distance away,

they must have long tendons to transmit the force they exert; the wrist is full of these tendons.

We may make a preparation consisting of a muscle and a nerve. The best known of such preparations is the gastrocnemius-sciatic preparation of the frog (see fig. 1). The nerve can be stimulated by an electric shock, a message passes along it, and if the muscle is still connected to the nerve, the fibres of the muscle receive the messages from their individual nerve-fibres and respond. The nerves are not part of the muscle, they make some kind of contact with it, at the nerve-ending (Plate VI, *a* and *c*), but that contact can be broken by various things, of which perhaps the most interesting is the drug curare, an Indian arrow poison which causes paralysis by blocking the contact between the nerve-ending and the muscle-fibre. Fatigue also has the same kind of effect, but in a less degree. Even, however, when the nerve is completely blocked, it is possible to excite the muscle directly by an electric shock. The wires carrying the current are laid directly on the muscle. Muscle is not as excitable as nerve. In other words, it requires a stronger shock than nerve to excite it; still it responds very well, and much of the work that has been done on muscle has employed direct electrical stimulation of the muscle-fibres. Let us examine what happens when a muscle is excited, either directly or through its nerve, by a single electric shock.

The visible thing that happens is a twitch. The muscle shortens if it can and moves a weight hanging on it; if the weight is too heavy to move the muscle stiffens and exerts a greater force. Then the muscle relaxes, lets the weight down again, and its stiffening and tension disappear. This, however, is not all. By means of delicate instruments it can be shown that the temperature of the muscle rises; in fact, in a single twitch it rises about $\frac{3}{1000}$ of a degree Centigrade. If we examine it still more closely we find that heat is produced not only while the muscle is contracting and relaxing, but for a long period afterwards, in fact, one and a half times as much heat is liberated after the contraction is over as during it. *Activity*, as we shall see more in detail later, is followed by a prolonged process of *recovery*. If we look into the matter further we find that oxygen is consumed, carbon dioxide produced, and sugar burnt. Finally, it is easy to prove that during its contraction the muscle is electrically active, just as a nerve is. An electric wave moves along it at high speed, and this can be recorded, as was mentioned earlier, while it passes the electrodes by which a galvanometer is brought in contact with the muscle.

Perhaps the most striking thing about an isolated muscle is the way it can be fatigued. If we stimulate it once every second its contractions will become

slower and slower, and weaker and weaker, until in a few minutes it will cease to be able to contract at all. It is easy to arrange that all these contractions shall be recorded on a drum at the same place, or one above the other. In fig. 18, for example, we have the record of a muscle writing with a lever on a revolving drum, the muscle being stimulated once for each revolution of the drum at the same point

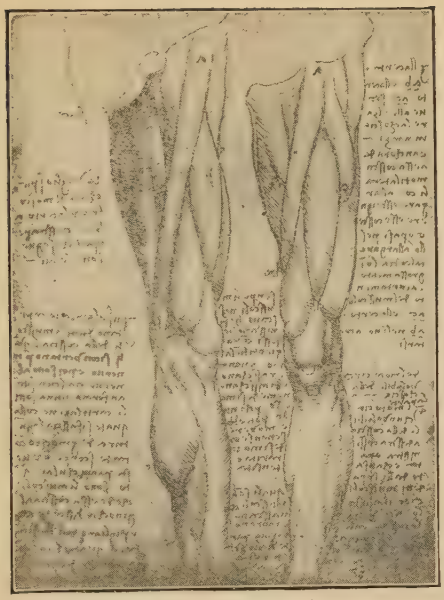
FIG. 18.—Record of muscular contractions. Time tracing below=100 per second (Halliburton).

P. Its first contractions are the tall narrow curves; as it gradually becomes fatigued the contractions become weaker and slower, until in the end practically no response is visible. It is noticeable that the first effect of fatigue is a slowing of the contraction rather than a weakening of it. Those of us who have run in races know how, at the end of a race, the difficulty is not so much that our legs feel weak as that we cannot get them to move quickly enough. This fatigue is a very striking thing and has long interested physiologists, and its study has been the

chief reason for recent advances in our knowledge of how the machinery of a muscle works.

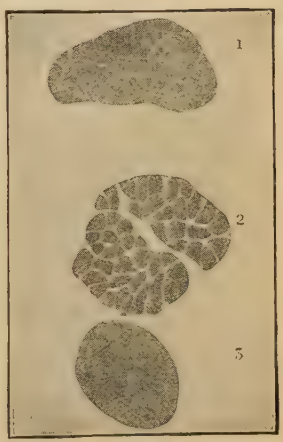
If the two legs of an anæsthetised animal be prepared, so that two corresponding muscles (one in each leg) write records on the same drum when their nerves are stimulated by the same shocks, we find that they fatigue at the same rate if they are treated in the same way. If, however, the artery supplying blood to one of them be clamped so that the blood to it is stopped, we notice that fatigue comes on very much more rapidly in the muscle of the bloodless limb; whereas the muscle supplied with blood goes on contracting for a long time—indeed almost indefinitely—the bloodless muscle will have reached a stage of complete paralysis in a few minutes. We know, of course, the same thing in ourselves. A violent and continuous effort in a small group of muscles—such, for example, as holding the body up with arms bent on rings in a gymnasium—largely hinders the free supply of blood to the muscles by pressing too heavily on their arteries and veins. In that case fatigue comes on, to the stage of almost complete exhaustion, within a minute, whereas when the limbs are moving and the muscles free, and the blood circulating easily through them, quite violent efforts may be made and exhaustion may not occur for a long while.

The importance of the circulation in this connec-

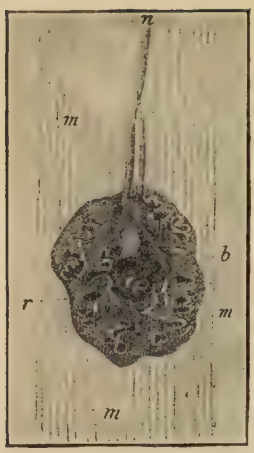


(*a*) Voluntary muscles of the human leg, from a drawing by Leonardo da Vinci (p. 43).

(*b*) Voluntary muscle-fibres (× 100) viewed at right angles to their length. Note cross-striations which are generally associated with voluntary muscle, but about which little is definitely known (p. 45).



(*c*) Cross-section of voluntary muscle-fibre (× 900). Note that the fibrils occur in bundles, though this may be artificial (p. 45).



(*a*) Motor end-organ. The nerve-fibre, *n*, comes down to the muscle-fibre, *m*, and spreads out upon it; a "bed" or "sole," *b*, lies between the branches of the nerve and the surface of the muscle (pp. 46, 55). (*Kühne.*)

(*b*) Lifting a weight in the hand, palm upward. *o*, biceps; *oo*, deltoid; *ooo*, brachialis. . . brachioradialis. The biceps and brachialis are exerting nearly all the lifting force (p. 71).

(*c*) Microphotograph of muscle-fibres with motor end-plates, *a* and *b*, lying on them. *a* is the ending of a medullated, *b* of a non-medullated nerve-fibre (pp. 47, 55). (*Kulchitsky.*)

tion can be shown in another way, namely, by a comparison of the fatigue which comes on in an isolated muscle stimulated through its nerve with the absence of fatigue in a human arm muscle stimulated as in Plate VII by means of shocks applied to the ulnar nerve. The isolated muscle stimulated once a second shows obvious fatigue in a minute or two; the human muscle, stimulated at the same rate, or even much more frequently, shows no fatigue for a long time. Why is it that the supply of blood is so necessary for the avoidance of fatigue?

Various explanations seem possible. For example, the blood might be bringing to the muscle-fibres some foodstuff to supply them with the energy they require. As a matter of fact the muscles contain within themselves large stores of food sufficient for long periods of activity. Or again, the blood might be carrying away some harmful substance produced by the muscles during their contraction. That this, however, is not the most important factor is shown by a further experiment. If we take two thin isolated muscles, with no blood supply at all, we can repeat exactly the same experiment by depriving one muscle of oxygen and giving the other all that it requires. Oxygen, as you know, is that constituent of the atmosphere which combines with things when they burn. The heat produced and the work done by animals, just as is the case with other machines,

comes from combustion, the burning of foodstuffs, within the living cells. If we blow oxygen into the chamber containing one of the muscles and nitrogen into the other (to keep out oxygen) we find that the muscle in oxygen fatigues only gradually, and then only to a certain level (never to complete exhaustion), while the muscle in nitrogen ceases altogether to function within a few minutes (see fig. 19). There

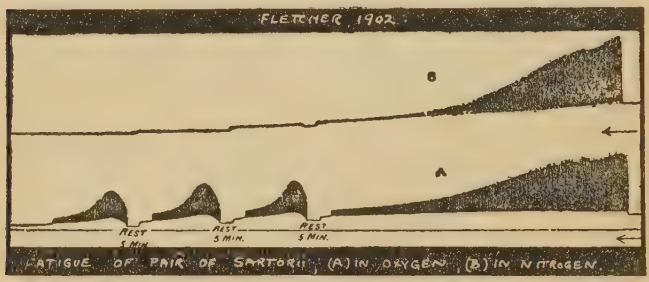


FIG. 19.—Twitches recorded on a very slowly moving drum, showing fatigue of a pair of sartorius muscles of a frog responding to the same sequence of stimuli once every second. A was in oxygen, B in nitrogen. B fatigues completely and ceases to respond, while A goes on contracting. After a rest, A responds more vigorously, while B shows no recovery at all. (Read from right to left.) (W. M. Fletcher.)

is no doubt, therefore, that *the main reason for fatigue is the absence of oxygen*, and we are led to ask how the oxygen prevents the fatigue, and to what processes or substances fatigue is due.

The answer to this question came from the chemical study of muscles. All living cells are really chemical machines, and we can never understand them properly until we know the nature of the chemical processes which go on inside them. It might have been imagined that by looking closely

at a muscle-fibre under a microscope we should have been able to find out something about the nature of its machinery. For generations people have examined muscle by such means, but with little result. Various things have been seen in muscle, various theories have been invented relating the structures observed to the behaviour of the machine. Many muscles, however, possess none of these structures; some of the smooth or involuntary muscles described in the next lecture are almost entirely devoid of the microscopic peculiarities on which theories have been based, yet they can contract just as well as the other muscles. The truth would seem to be that the real machinery of the muscle is far too small to see; it is, so to speak, of molecular dimensions. When a crystal forms the molecules set themselves in some special order or arrangement. Probably it is the same with a muscle: when it is excited its molecules fall into a new orderly arrangement, tending, like a piece of india-rubber, to shorten to a new length. It is this molecular smallness of the mechanism underlying all movement in animals which makes the problem so difficult. If we could see the bits of the machine it would be easier to fit them together into a scheme. As it is, the properties of a contracting muscle seem to depend upon obscure chemical properties of unknown chemical substances, which tend, for unknown reasons, when we

stimulate the muscle, to fall into some new orderly but unknown arrangement.[1] One thing, however, would seem certain, namely, that the machinery is chemical in nature.

In the case of muscles there are many chemical bodies involved. The muscles themselves are made of protein, a substance built up of carbon, hydrogen, nitrogen, and oxygen, together with traces of other elements. They contain salts and, of course, water, together with fat-like materials and a number of chemical bodies whose function we do not yet know. In particular, however, they possess a store of a starch-like substance, glycogen, which readily breaks down into sugar, just as starch can be made to do. This glycogen is the fuel which the muscle uses for its activity, and it carries a store of it about, just as automobiles carry gasoline in their tanks. In a starving animal there is only a little glycogen, but there is always some. Without it an animal would be unable to move at all. Glycogen is used up during work, but it is restored again from sugar coming to the muscle-fibres through the blood. The blood gets the sugar either from the liver, where it is kept till needed, or from the intestines, where it

[1] These arrangements are probably similar to those of the molecules or atoms in a crystal. India-rubber shows a crystalline structure when subjected to tension. In this sense a muscle probably "crystallises" when it contracts.

is absorbed from the food during digestion. It seems probable that muscles cannot use directly any fuel other than glycogen or sugar. Of course in our food we take many other things which are all very useful and necessary, but they have to be transformed into sugar—for example, by the liver—before the muscles can use them. It is just the same with an automobile; it requires gasoline or benzole for its engine, and if we have nothing but coal supplied to us we have to distil the coal and prepare the benzole from it before we can make the engine go.

Another substance has been found in muscle, also of great importance in this connection namely, lactic acid. When milk goes sour, lactic acid is produced from milk sugar by the agency of the lactic acid bacillus, which develops there, especially at a high temperature. This lactic acid is the cause of the souring, and of the clotting which follows it. In muscles also lactic acid appears, not in this case by means of a bacillus, but by the machinery of the muscle itself. When a muscle contracts a certain amount of lactic acid is liberated in it, in proportion to the amount of work done by the muscle. As you will hear in a later lecture, very considerable amounts of lactic acid may be set free in the muscles of a man during hard work. An ounce of it may easily be formed when a man runs 100 yards as fast as he can. Now lactic acid is a pretty strong reagent, and there

is no doubt to-day that fatigue [1] is due mainly to its formation in the inside of the muscle-fibres. The function of oxygen is to remove the acid, once it has been formed.

It would seem very likely that the immediate source of the lactic acid is an unstable chemical substance formed by reaction between potassium phosphate and glycogen. The very important chemical processes involved are being vigorously investigated at the present time, and in the near future it may well be possible to speak much more definitely about the chemistry of muscle than it is to-day. As yet, however, we cannot say much about this phosphate story.

We must picture the muscle as being like a storage-battery or accumulator. A lead accumulator consists of lead plates and sulphuric acid. When we connect its terminals to a lamp or motor, it supplies current and it runs down, sulphuric acid passing from the solution into the plates. When it is completely run down it has to be recharged (it is better if we do it earlier), and this recharging consists of putting back the sulphuric acid from the plates into the solution and restoring the lead of the plates

[1] The word 'fatigue' covers a multitude of different things, some real, some imaginary. In these lectures and in this connection it implies the very real effect which follows severe muscular effort.

to its condition as metal or oxide. In this process of recharging the accumulator a dynamo must be used to supply the electric current, and a motor of some kind must run in order to drive the dynamo. This motor requires fuel and oxygen, otherwise it cannot find the energy to turn the dynamo. Thus fuel and oxygen are required to recharge the accumulator after it has run down, whereas during the actual process of running down—that is, of providing a current—the accumulator for the time being requires no fuel or oxygen at all.

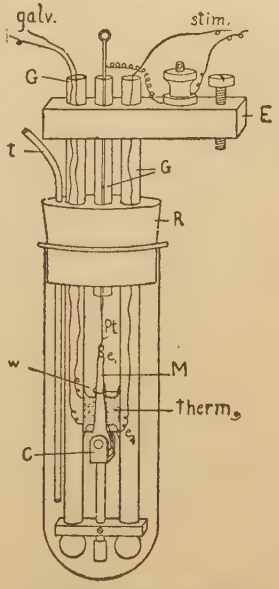


FIG. 20A.—The thermopile in its chamber with a pair of sartorius muscles (M) lying on its "hot" junctions. The rise of temperature of the contracting muscles warms these junctions and sends a current to the galvanometer which deflects (see also fig. 4) (Fenn).

The analogy of the accumulator is a very close one and helps us to understand the processes of fatigue. The muscle can work for a while without any oxygen at all, but it rapidly gets run down and has to be recharged. If there is still no oxygen available, the machine required to carry on the recharge cannot be started up, and the muscle remains run down and unable to do any more work. In the accumulator the appearance of sulphuric acid in the

plates is a sign of the running-down process; so in the muscle the appearance of lactic acid in the fibres is a signal of fatigue: both have to be

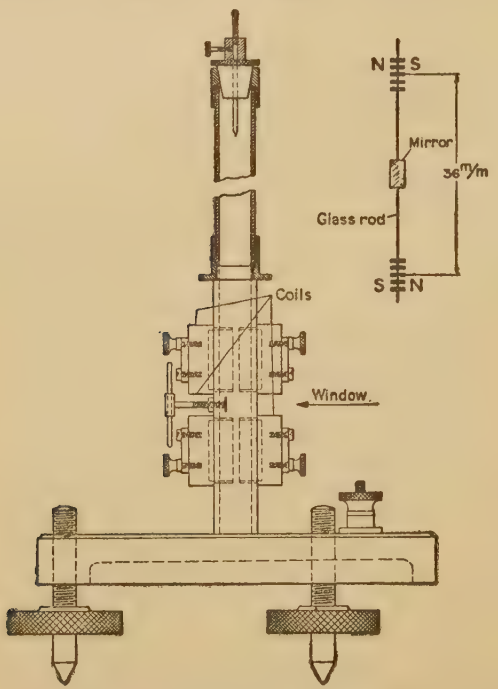


FIG. 20B.—The galvanometer which records the current. This has to be very rapid in its movements, as well as very sensitive. The moving part, which weighs only about 5 milligrams ($\frac{1}{6000}$ oz.) consists of 10 little magnets on a glass rod carrying also a mirror to reflect a beam of light. The whole is borne by a quartz fibre about $\frac{1}{25000}$ in. thick. When a current runs through the coils of a galvanometer, it twists the magnets round and a beam of light, reflected from the mirror, moves on a scale (Downing).

replaced in their original positions, the sulphuric acid into the solution, the lactic acid as glycogen, before the fatigue can be recovered from or work can be started again.

In the recharging process in muscle, therefore,

oxygen is used—that we can easily find by experiment on ourselves, as I shall show in a later lecture; carbonic acid is produced; a little heat, though many times greater than that produced by nerves, is liberated, as can be shown by delicate electric apparatus (figs. 20A and 20B); and a certain amount of fuel is burnt to supply the energy for the recharge. This fuel seems to be either glycogen or sugar, which gradually disappears from the muscle during a long bout of work—unless it be replaced from the blood. During the recovery process the lactic acid vanishes, but is found over again in its original form as glycogen. We may summarise the matter as follows:—

Contraction

Glycogen——→lactic acid+energy.

Recovery

Lactic acid——→glycogen–energy.

Glycogen+oxygen——→carbonic acid and water +energy.

In the isolated muscle, at the temperature of the room, this recovery process takes about 10 or 15 minutes, provided there be a plentiful supply of oxygen; if the supply of oxygen be poor the process takes longer. As we raise the temperature all vital processes go on more quickly, and among them the recovery process quickens also. At a low temperature the recovery process is very slow; it must take a

frog, outside on a frosty day, almost an hour to recover from a few jumps. Perhaps fishes who live in cold water have improved their chemical machinery so as to recover more quickly; if not, they also must spend a large proportion of their time in recovering from any sudden efforts they may feel called upon to make. At a high temperature, however, the process is rapid, and one of the advantages of the high temperature of man and of other warm-blooded animals is the greater speed at which the recovery process after exercise can go on. From moderate exercise, recovery in man takes only about five minutes; from severe exercise it may occupy much longer, until after the most exhausting exercise which a man can undertake—even when he is "in training"—it may be an hour or more before he is completely restored.

Muscles are machines in many respects like those which we employ to do our work, but in some ways they are superior to other machines. Their most obvious advantage is that they need no looking after: they need not be oiled or adjusted; they do not require cleaning or repair; they go on for many years without any attention whatever; they are very superior machines. They are also very efficient. By "mechanical efficiency" an engineer means the proportion of the energy which he puts into the machine that can be turned out as useful mechanical

work. If a steam-engine has a 10 per cent. efficiency it will supply 10 units of useful work for every 100 units of energy with which it is provided. The efficiency of a muscle, measured by the ratio of the mechanical work which it can do to the energy of the fuel (foodstuffs) with which it is provided, may be 25 per cent. or more, if it be properly loaded, and allowed to work at a suitable speed, which compares quite well with the best machines of human manufacture.

Mechanical Efficiency

Steam-engines without condensers . .	about $7\frac{1}{2}$ per cent
Steam-engines with condensers . . .	9 to 19 "
Gas-engines	14 " 28 "
Diesel engines	29 " 35 "

The efficiency of the muscle is an important thing, as we shall see later, when we come to calculate the amount of work the body can do when provided with a given amount of food. It is also of great interest theoretically. Its high value shows conclusively that the muscle-fibre is not a heat engine: to attain an efficiency of 25% a heat engine must have a difference of temperature of at least 100° C: such a thing is inconceivable in a little fibre only $\frac{1}{500}$ inch in diameter. The muscle is a chemical machine working at constant temperature.

Muscles are enormously strong. Even the isolated muscle of a frog, which is not a very strong animal,

can exert quite astonishing forces: it may easily lift a thousand times its own weight. In ordinary life we do not notice the enormous forces which muscles can exert. In a limb they are usually working at a great mechanical disadvantage; they are pulling very close to the fulcrum of a lever, whereas

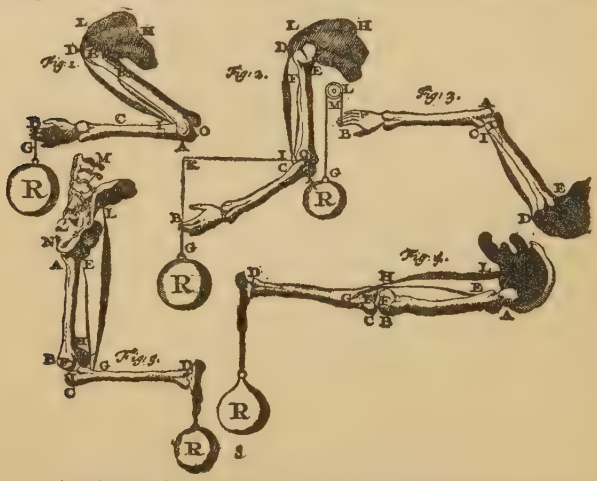


FIG. 21.—Attachment of the muscles to the bones and the leverage exerted. 1–3, the human arm; 4–5, the leg (Borelli, *De motu animalium*).

the load may be 10 times, or more, as far away (see fig. 21). Sometimes, however, the mechanical disadvantage is not so great—for example, in the jaw of a fish or in the claw of a lobster,—and the force that can be exerted is correspondingly greater. In most cases animals work on a very high gear; they have sacrificed strength in order to secure speed of movement. In some cases, however, as in the jaw, speed is not so necessary, while strength is all-

important and the gear-ratio is less; then we can see more directly the very powerful forces which muscles can exert.

Most small boys know the appearance of the biceps of the arm. Strong men who advertise in newspapers exhibit their biceps to an admiring public. The biceps, however, is not the only muscle involved in a simple flexion of the arm: indeed, it is rather occupied with such things as turning a screw-driver (clockwise in the case of the right arm, counter-clockwise in the case of the left). When a weight is lifted by a bending of the arm (Plate VI, *b*) the palm of the hand being upwards, the work is done largely by the brachialis anticus; when the palm is downwards the biceps does no work at all. The biceps and brachialis anticus muscles together, of the arm of a fairly muscular man, have been found to weigh about half to three-quarters of a pound. In a single contraction of the muscles of such a man work may be done sufficient to raise a $\frac{3}{4}$-lb. weight 100 feet into the air—not a bad record for a high jump!

These muscles are working at a mechanical disadvantage of about 10 to 1; in other words, they are pulling on a lever (the bone) at a point very close to the fulcrum, so that the load is 10 times as far away. In an ordinary healthy man they are capable (in the two arms together) of holding a weight, even with this mechanical disadvantage, rather greater

than the weight of the man himself, not perhaps of holding it for long, but certainly for a few seconds. Let us assume that they can hold a horizontal rod weighing 200 lbs. for a second or two. The mechanical disadvantage is about 10 to 1, so the force of the muscles must be ten times this, namely, about 2000 lbs.—1300 to 2000 times their own weight, not far short of a ton!

This strength of muscles is the more remarkable when we remember the material of which they are made—a jelly-like substance with very fine membranes covering the individual fibres. With such a material the factor of safety cannot be great, and we find not seldom, especially in athletes, that the muscles tear and the tendons break when subjected to excessive strains. Part of the stiffness and soreness which result from violent exercise, when we are out of training, is very likely due to actual mechanical tearing or injury of some of the fibres and membranes of the muscles. Bruises are certainly due to mechanical breakage of the tissues and blood-vessels, which appear to be much stronger in some persons than in others.

The voluntary muscles differ from one another enormously in speed. The slowest cross-striated muscle known is one which works the gastric mill of the crayfish. The stomach of the crayfish has a machine for grinding up his food, and this machine

is operated by a muscle which may take half a minute or more to give a single twitch. Even the leg muscles of the tortoise, especially after he has been having his winter sleep, may be very slow. I once met a tortoise whose biceps cruris muscle took more than half a minute to complete a single contraction. At the other end of the scale we come to some muscles of amazing quickness—those that work the wings of

FIG. 22.—Record of the beats of the wings of a wasp, held near to the surface of a rapidly moving smoked drum, and struggling to fly away (Marey).

insects. We can recognise a mosquito from the high pitch of the note given out by his wings as they beat the air. Buzzing flies, wasps, and bees have each their characteristic sound. The pitch of a note betokens the number of vibrations per second of the air through which it comes.[1] In the case of some of these insects the wings are going 300 times or more per second, 10,000 times as fast as the crayfish, or that particular tortoise I referred to.

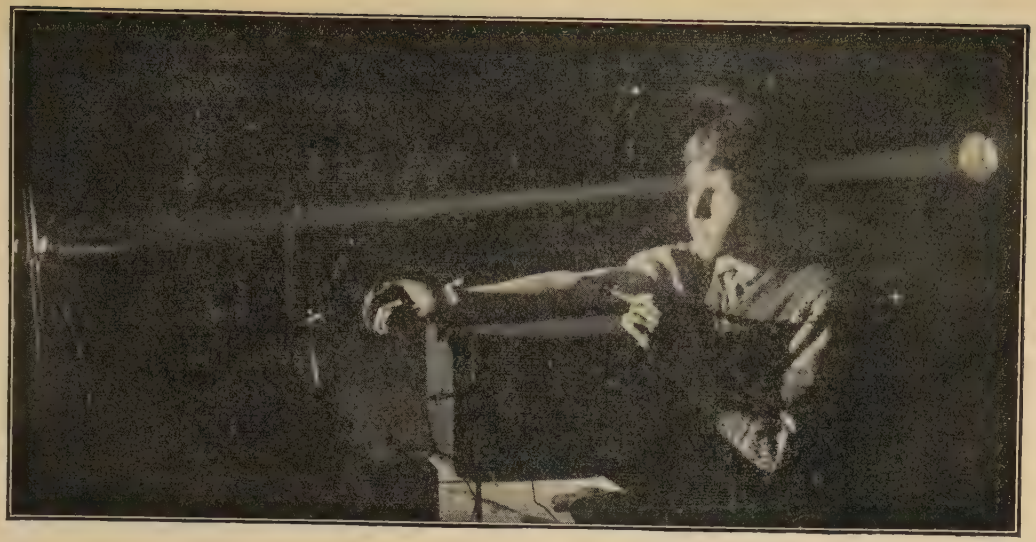
Between these two extremes we find every kind of muscle and every variety of speed. Little birds are amazingly quick in their movements; the sloth

[1] That the speed really corresponds to the pitch of the note was proved by Marey, who allowed the beating wings of an insect to write on a rapidly moving drum, so that he was enabled to count the beats (see fig. 22).

is amazingly slow; in general the smaller creatures are the quicker. Even in a single animal—for example, in ourselves—the movements vary greatly from one part of the body to another. The muscles that work the eyelid move extremely rapidly in order to protect the eye from harm; they are allowed to shorten so rapidly because the object they move is so small and light. On the other hand, try as we will, we cannot move our arms or fingers more than 10 times a second, and even so the movements are only very little ones, more like an incomplete tetanus (see fig. 16) than separate contractions. We may congratulate ourselves on our quickness as compared with a tortoise, a lobster, an elephant, or an ox, but we make a pretty poor showing when compared with a wasp or a mosquito, or even with a robin or a squirrel. Why should we not move faster? Why, in a world where quickness is so essential, where in the struggle for existence rapidity of movement even more than strength may be the determining factor, should we not have developed muscles as rapid as those of insects. The answer is quite simple: if we did so, we should break.[1]

The muscles of the wasp's wings are very short, but if they were 10 times, or 100 times, as long they would take no longer to contract. The time taken in a contraction depends not on the length, or

[1] See also Lecture VII.



Stimulation of the ulnar nerve by condenser discharges, and recording of the movements of the little finger by reflection of a beam of light from a mirror to which the finger is attached (pp 27, 47, 52).

(*b*) Man deprived of [illegible] muscles better.
(*c*) With only a few muscles left.
(*d*) After a layer of the [illegible] has been taken off.
(*d*) Deprived of all his muscles (p. 77).

breadth, or thickness of a muscle, but only upon its intrinsic qualities. If each millimetre of a muscle-fibre took $\frac{1}{100}$ of a second to shorten, then if there were 100 separate millimetres of muscle in a row, each shortening in $\frac{1}{100}$ of a second, the whole muscle also would shorten in that time, if they all started off together, as they actually do. Let us try to imagine what would happen if we could shorten our muscles, if, for example, we could raise our arms in $\frac{1}{100}$ of a second.

To make it clearer, let us take a *long* glass rod. It can be swung backwards and forwards, provided that it be not moved too quickly. Let us take it by one end and slowly wave it from side to side; its inertia is not sufficient, at a low speed, to put any great strain upon it. Let us, however, try to wave it across rapidly; it snaps off sharply just beyond one's hand. Let us now take a *short* glass rod and try the same experiment again. We may move it as rapidly as we like, we may jerk it and shake it, and it remains intact. To make the experiment properly, if we take a glass rod $\frac{1}{4}$ of the length we should also take it $\frac{1}{4}$ of the thickness. Let us do so. We find that still it will not break, however rapidly we wave it round. The experiment is simple and obvious, but it gives us the answer we require.

An animal is made of very breakable material. It is easy to snap the muscle-fibres, the tendons, and

the bones. Just as any engineering structure is built with a certain factor of safety, so we are too: Nature is just as sound an engineer as you can find in America, and learnt millions of years ago the same lessons as engineering students learn to-day. It would obviously be a very good thing if we could move faster; just as obviously it would be a very bad thing if we broke whenever we moved. Our present state is a compromise between the two. It is not unusual for an athlete to tear a tendon, or to strain a muscle, and not unknown even for him to pull a piece off a bone by an exceedingly violent effort. We are obviously not far from our limit of safety. If we doubled our speed of movement, the number of strains and breakages would increase very many times, and athletics would become a highly dangerous pastime. Arguing, therefore, from the case of the glass rod, we now can see why smaller animals can have a greater quickness of movement. A squirrel is $\frac{1}{12}$ as long as we are, and I imagine that his bones are about $\frac{1}{12}$ as thick as ours. Our experiment with the glass rod teaches us that it would be safe for him to move many times as often as we can in every second; in fact, theory suggests 12 times as often. Actually we know how extraordinarily rapid are his movements. What he loses in length of stride he gains in frequency. A little

dog can run very nearly as fast as a big dog by moving his legs more often.

In the past there used to be gigantic animals on this earth; awkward creatures they must have been and very slow. The same factors which prevent us from moving as rapidly as a robin or squirrel must have prevented one of these great animals from moving as fast as we can. If his enemies were small and active, it must have been very difficult and trying for him to have to deal with them. If he did not move quickly enough he would lose in the struggle for existence: if Nature allowed him to move too quickly he would break.

Note.—On Plate VIII are four pictures from a book on anatomy by Albinus, a Professor of Anatomy and Surgery at Leyden, published in 1747. (*a*) shows a man deprived of his skin to exhibit his muscles better; (*b*) shows him after a layer of the outer muscles has been taken off; (*c*) leaves him only a few muscles; and (*d*) none at all.

LECTURE III

The Heart and some other Muscles

THERE are very many kinds of muscles in an animal, as well as those which move his limbs. Some of these are voluntary, they respond to the will of their owner; such, for example, are those which move our eyes, such is the diaphragm whose contraction expands our lungs and whose relaxation allows them to collapse. There is the little ring of muscle which focusses the lens of the eye; there are the muscles that close the shell of a shell-fish, and those that hold it closed; there are those that pull out the little spots on the body surface of the cuttle-fish, and so enable him to change his colour. Not all of these are, strictly speaking, voluntary, and many of them, in appearance and in character, are much more like the involuntary muscles whose movements are automatic. For example, the ciliary muscle of the eye, whose contraction releases the lens and allows it to bulge, so giving it greater focussing power, is composed entirely of smooth fibres, and the nerve which brings it orders is similar to those which run to involuntary muscle. Yet in a sense this muscle is voluntary; we can focus our eyes when and how we like. The only obvious difference from a limb

muscle is that when we do so it does not seem that we send direct orders to focus to the eye, but merely "look" at a thing at some definite distance and the focussing follows automatically. The diaphragm, however, in structure and innervation is like an ordinary voluntary muscle; yet it goes on working continuously and automatically even when we are asleep. When we come to some of the lower animals the question of whether a muscle is voluntary or not becomes almost a matter of opinion. How far can we talk of the "will" of a mussel, or of the "voluntary" movements of an oyster? We can only argue by analogy with the higher animals, and in general we are apt to describe as voluntary those movements and functions which deal with the external world, and as involuntary those which are concerned with the domestic arrangements of the animal. In this sense the muscles which work the foot of *Mytilus* (the common sea mussel) and those which close and hold fast the shell of *Pecten* (the scallop) are voluntary, although we find that they differ widely in appearance and structure from the voluntary muscles of man. Some of these muscles are cross-striated; many, however, are unstriated, and it is impossible to put them into any very definite category on either side. One of the most beautiful of these border-line muscles is that which works the spots of *Sepia* (the cuttle-fish) or of his relative

Loligo (fig. 23), or his distant connection *Octopus*. These animals swim about freely in the water—you can see them at the Acquarium—and they possess

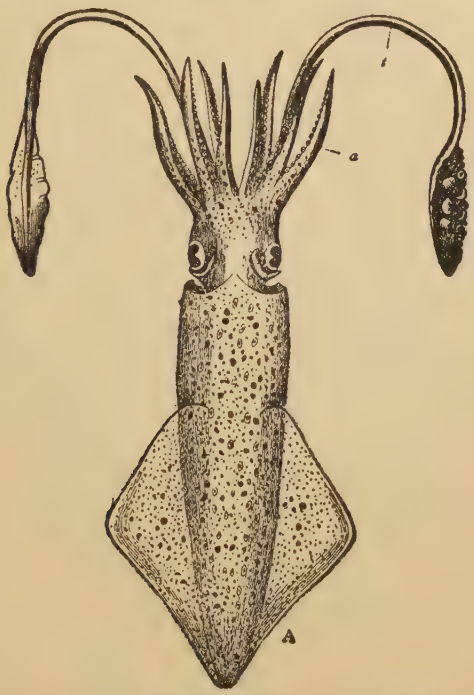


FIG. 23.—*Loligo*. (*a*) arms; (*t*) tentacles. Note the spots covering the body, some expanded, some contracted. *Loligo* has a "funnel" or muscular tube on the lower side of its body by which it squirts out water in a series of jets, so driving itself backwards through the sea. It has also an ink-sac, containing a large amount of a carbonaceous pigment which it expels into the water as a means of concealment.

the strange faculty of being able to change their colour in a fraction of a second. They are covered with hundreds of little dark spots (fig. 24): running out radially from each of these are muscle-fibres

which, when they contract, stretch out the spots to many times their original size, and so entirely change the colour and to some extent the appearance of the animal. They are strange creatures: in addition to their spots they possess a bag of very potent black ink, which, when provoked, they

FIG. 24.—Change of colour of *Loligo* or *Octopus*. On the left the spots have shrunk up, the muscles running out radially having relaxed. On the left the spots are pulled out by the contraction of the muscle-fibres, the process occupying only a fraction of a second. Note: there are far more muscle-fibres than shown, the four allowed to each spot being for illustration only.

squirt out into the water and so create a cloud in order to confuse their enemies. As Dr. Pantin of Plymouth once described it: "You see a strange-looking white creature coming along. If he is annoyed, or if he wishes to establish an alibi, he suddenly emits a large cloud of black ink and emerges from the cloud no longer white but brown or pink." No more complete alibi could be wanted. If he is in a tank and you touch him, you see a wave of colour pass across him, almost like a cloud travelling rapidly over a field. Sometimes even, especially when he is feeling rather low, you can watch his spots beating like so many little hearts. The muscles that work these spots are, I suppose, voluntary. At any rate

they contract immediately when the animal is excited; though it is not easy to say whether such an animal possesses a "will" or not. In spite, however, of their apparently voluntary nature, and of the great quickness of their response, they have a microscopic appearance quite unlike that of voluntary muscle in man. Thus we see that, although it is useful to have the main categories of voluntary and involuntary muscle, it is not always possible to place any particular muscle in either class.

Of muscles that are definitely involuntary there are many examples. The most obvious perhaps are those which work our digestive apparatus. The microscopic appearance of these is shown in Plate XI, *a*. Let us start at the top with the œsophagus or gullet. Around the gullet is a muscular coat, which in the upper third is composed of striated muscle-fibres, the lower two-thirds being of the plain variety. Corresponding to this, when we swallow, the upper part of the throat responds more or less to the will, while the rest reacts automatically to the stimulus of down-coming food. There are two layers to the muscular coat—an outer layer in which the fibres run lengthways, and an inner in which they have a circular arrangement. In the stomach there are three layers of plain muscle-fibres, over which we have no direct control whatever. These muscles by their movements churn the food,

and when the stomach is empty close it right up. The pangs of hunger, very noticeable in healthy hungry animals at the sight of food, are due to involuntary movements of these muscles. When the food is sufficiently digested in the stomach a sphincter muscle, which guards the entrance to the intestine, relaxes for a moment and a certain amount of the partly digested gastric contents is squeezed forward. As digestion proceeds, the opening of the pyloric sphincter becomes more frequent, until finally the stomach has emptied itself into the intestine and takes the form no longer of a bag but of a long curved tube.

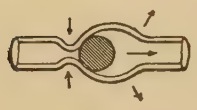


FIG. 25.—Diagram showing peristaltic contraction of the intestine. A wave of relaxation, followed by one of contraction, travels along the intestine forcing the contents forward (Cannon).

In the intestines the same kind of process goes on. "Peristaltic waves," as they are called, run down them, stirring the food and gradually working it along (fig. 25) until finally it reaches the lower end; by then all the useful constituents of it have been digested and absorbed and nothing but refuse is left. All these movements from one-third of the way down the gullet to the end of the intestine are due to involuntary muscles, working partly automatically, partly through the involuntary nervous system, but without any instructions from their owner.

These movements of the digestive apparatus can

be seen in portions removed from a dead animal, for they will work for long periods after such removal, just as the voluntary muscles do. Or they can be studied in an animal in which a celluloid window has been let into the wall of the abdomen. Such an animal—for example, a rabbit may live a happy and normal life, and so allow us to study the movements of his digestive organs, or the flow of blood through them, directly by watching them through the window. A third way, and perhaps the best way, to observe these movements is by using X-rays. These of course pass through the softer parts of the body, only the denser parts casting a shadow. The movements of the stomach and intestines cannot be directly observed without some further aid. For this purpose food must be mixed with the salt of some heavy metal for example, bismuth or barium. If a mouthful of milk mixed with bismuth carbonate

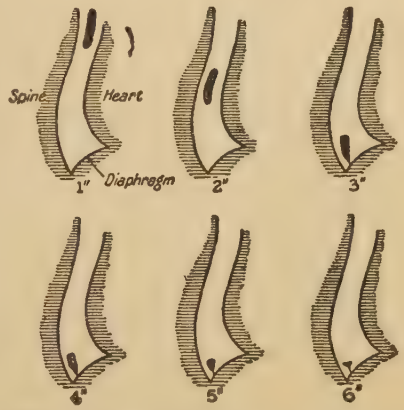


FIG. 26.—Diagram of the position of the shadow of a mouthful of an "opaque meal" (*e.g.* porridge mixed with barium sulphate) at intervals of one second after swallowing. The food passes rapidly to the bottom of the œsophagus and more slowly through the narrow cardiac orifice of the stomach (Cathcart, Paton, and Pembrey after G. F. Hurst).

or barium sulphate be swallowed, it will be seen passing rapidly down the gullet to the orifice of the stomach. Here the passage becomes slow and the fluid escapes slowly in a narrow stream into the stomach (fig. 26). It takes about six seconds for the milk which is swallowed to pass completely out of the œsophagus. If a small dry object be swallowed it may pass down the gullet with extreme slowness, and may take as much as fifteen minutes before it reaches the cardiac orifice of the stomach, although the individual who has swallowed it is quite unaware of its continued presence in his throat. If it be well moistened with saliva, or water, it passes much more rapidly, reaching the stomach in eight to eighteen seconds.

The movements of stomach and intestines can be followed by similar means. A living unanæsthetised animal (or a man) is given a meal, for example, of bread and milk mixed with a quantity of a bismuth or barium salt. This salt does not interfere with digestion, but makes the contents of the stomach opaque to X-rays. The waves of movement passing along can be seen, the gradual diminution in the size of the stomach during digestion recorded. The further voyage of the food down the intestine can be followed, the portion of food containing the bismuth always casting a dark shadow on the screen. Such observations can be made on human subjects,

and in medical schools it is a usual thing for students to volunteer to take an "opaque meal," in order to allow these movements to be demonstrated to their class. In hospitals the method is commonly used, in order to observe the movements, size, or position of the digestive organs.

In Plate IX, are shown four X-ray pictures of the stomach and intestines of a human subject after partaking of an "opaque meal." Each exposure was about $\frac{1}{4}$ of a second, and the figures shown are negatives of the original photographic records. The opaque meal stops the X-rays from penetrating the stomach or intestines, in which it lies, so that on the original plate these come out white; all the denser parts of the body, such as the bones or the thicker muscles, cast a shadow on the plate, which comes out lighter therefore in these places. In a negative taken from the original plate these lighter parts come out darker, and we get the appearance shown in Plate IX. In each photograph the vertebræ of the spinal column can be plainly seen, and in some of them the bones of the pelvis also. (*a*) was taken immediately after the opaque meal. In the figure the stomach is the long dark bag, with an obvious air-space at the top where it is not quite full. Behind it, in the lower half of the picture, is a shadowy appearance which represents the intestine, still slightly dark from a previous opaque meal.

The pyloric opening from the stomach into the intestine, which relaxes at intervals and allows the food to pass on, is indicated by a very small arrow in the lower half of the figure. (*b*), taken two hours after the meal, shows the stomach already two-thirds empty, the food having passed on, as shown by the lighter shadow, into the duodenum and the jejunum. (*c*) shows the stomach already practically empty, and little food now left in the earlier part of the small intestine; the black shadow has passed further on. (*d*), taken seven hours after the meal, shows the whole of the food now in the lower part of the intestine. The actual movements which carry the food along can be seen on the screen of the X-ray apparatus. In the figures we can only observe the effect of these movements at long intervals, as recorded by an instantaneous photographic exposure. Even so, however, the considerable change which has taken place in the appearance of the food during the seven hours covered by Plate IX, shows the effectiveness of the involuntary muscles which churn up the food and move it forward in orderly array through the alimentary canal. The movements are involuntary, they are entirely out of our control, but if by chance they go wrong, we soon realise how important they are.

There are many other kinds of involuntary muscle. For example, all our blood-vessels are surrounded

by bands of such muscle, which remain in a state of "tonic" contraction, regulating the capacity of the vessels and so the pressure of the blood in them. These muscles are governed by nerve-fibres coming

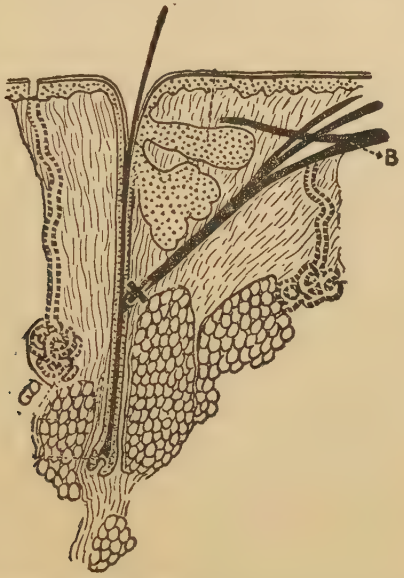


Fig. 27.—Vertical section through the skin showing a hair follicle. B. involuntary muscle-fibres pulling on the hair follicle at X, and causing the hair to stand on end when they shorten.

from the involuntary portion of the nervous system; their response is automatic, and adjusted—like an automatic carburettor—to the needs of the animal. Of other involuntary muscles there are several whose movements we are well aware of. The *arrector pili*, by contracting, causes the hair to stand on end (fig. 27). This contraction occurs when cold is suddenly

applied to the skin, or in various states of emotion. The contracted condition of all the muscles of the hair follicles is shown by the "goose-flesh" which we all know. Another case is that of the two layers of involuntary muscle which occur in the iris of the eye. One of these layers runs circularly round the pupil, and when a sudden strong light reaches the eye this muscle contracts and closes the pupil down to a pin-hole. The other layer of muscle is arranged radially, stretching from the outer attachment of the iris to the rim of the pupil, so that by its contraction it causes the pupil to open. On going into the dark, on accommodating the eye for distant vision, and under conditions of emotion such as anxiety or fear, the pupil is found to dilate.

The most striking characteristic of these involuntary muscles is the relative slowness of their movements. The processes which they govern, the domestic arrangements which they serve, do not so urgently require speed as the external activities of the animal. Consequently these muscles have adopted a slower and more economical rate. There are various other differences, but these are mainly quantitative and not differences of type.

It is common to describe the heart as a separate type of muscle not coming into either of the other categories, voluntary and involuntary. Actually it is involuntary in the sense that it is not governed

directly by the will, but in microscopic structure (Plate XI, *d*) and in other characters it approximates more closely to the voluntary type. The heart is an amazing machine; it is so well adapted to its purpose

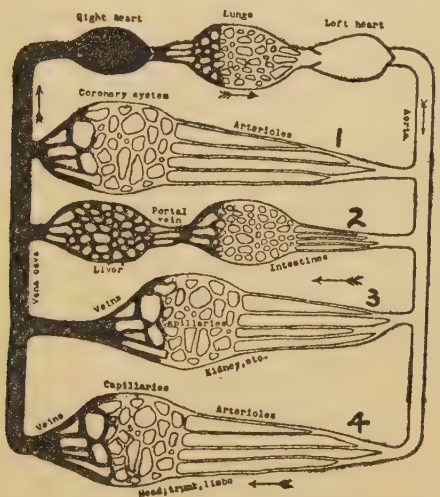


FIG. 28.—Diagram of the supply of blood in an animal (Bayliss).

and so capable of meeting the needs of the body in emergency. Its duty is a very vital one and if it goes on strike even for a few moments its owner dies. Its job is to pump blood round the body. Fig. 28 illustrates by a diagram the supply of blood in an animal. At the top are the heart and the lungs. The heart is shown, for clearness, as if it were two separate organs, a right and a left heart. Actually it is one organ, with two chambers, the blood passing out from one chamber through the lungs and back

to the other. The "venous" blood is shown dark, the "arterial" light. The venous blood lacks oxygen, which it takes up in the lungs, changing colour from blue to red in so doing. Note the valves at the entrance and exit of each chamber. The blood leaves the left heart and passes into the aorta, and so into the general circulation. There are four separate systems shown "in parallel." In that marked (1) the blood passes through the capillaries of the heart muscle itself, supplying it with oxygen and fuel. In (2) the blood passes through the intestines, absorbing digested food, and through the liver, which is the chief chemical laboratory of the body. In (3) the blood flows through the kidneys, where it is purified, and unnecessary or harmful substances eliminated. In (4) the blood goes through the muscles and other tissues of head, trunk, and limbs. After breaking up into countless capillaries, in each case the circulating blood comes together again into veins, reaching the right heart by the superior and inferior *venae cavae*. All the vital organs of the body need a continuous stream of blood, in order to supply them with foodstuffs for fuel and materials for growth and repair, but especially to provide them with oxygen. If the brain be deprived of oxygen, even for a few seconds, it (or its owner, whichever way you like to look at the matter) passes into unconsciousness. So near are we all to the end of

things material: so immediately dependent on a simple chemical substance—oxygen.

The amount of blood circulating is fairly large: in a man at rest it may be about 4 litres a minute —nearly a gallon, about equal to the total amount of blood in the body. This is nearly 500,000 gallons a year, about 30,000,000 gallons in 65 years, even in a man remaining continuously at rest—not a bad output for a little self-regulating pump weighing less than a pound. During muscular effort its output is greater, under conditions of severe exertion perhaps 8 times as great as during rest. During this pumping process the heart does a great deal of work. The pressure in the arteries is high, and equal approximately to that of about 5 or 6 feet of water.[1] Thus in a year the heart of a resting man does work equivalent to raising nearly 500,000 gallons 6 feet upwards, or to raising 100 gallons to the top of Mount Everest. In a man doing average work the mean output will probably be twice as great, so that his heart in a year will do the work required to raise 200 gallons—that is, about 1 ton—from sea-

[1] In the case of an animal like the giraffe the blood pressure must, in some parts of his body, be much higher than in a man: there is a *difference* of pressure of 20 feet or so of blood between his head and his feet, and some strange reactions must occur in his circulation when he suddenly bends his head down. It would require an engineering workshop, however, and not an ordinary laboratory, to investigate them.

level to the top of Mount Everest. The matter can be expressed in an even more fantastic way: the work done by the heart of a healthy man would in five months be sufficient to lift it clean out of the gravitational field of the earth into empty space outside. The work done by his heart in 65 years would be enough to lift his whole body right away from the earth. Such calculations perhaps may seem trifling, but they may help to provoke the imagination of some who have not lost all the wonder of youth and make them appreciate the work of this little organ—the heart—whose behaviour has always been one of the most fascinating of human problems.

In Plate X are shown photographs of a model of the heart of a man. The heart lies more or less centrally in the thorax, but during its contraction it stiffens out towards the left side, where its beat can be felt on the body wall, or heard, either by putting the ear to the chest or by using a stethoscope. During "diastole" (while it is filling) it rests upon the diaphragm muscle below (see Plate XI, c); during "systole" (while it is contracting and forcing its blood out) it kicks upwards and to the left, giving a tap (the apex beat) on the chest wall. It is covered with a thin inextensible bag, the pericardium, which prevents it from expanding too far in filling. The right chamber (Plate X, *a* and *c*) receives blood from the veins, valves being provided

at the entrance and exit of the right ventricle, so that when the heart contracts blood is not expelled back into the veins, but on into the pulmonary artery. The right heart is nothing like as strong as the left heart, since it has only to force the blood round through the lungs and not through the rest of the body. Between the right and the left chambers there is a muscular "septum," which, before the days of Harvey, was believed (contrary to all evidence) to be porous, and to allow the blood to pass from one side to the other. The blood actually reaches the left chamber *via* the lungs. The left heart is shown in Plate X, *b* and *d;* it also is supplied with two sets of valves, and is strong and muscular, so that it is able to force out large quantities of blood at a relatively high pressure into the aorta. The path taken by the blood in the heart can be seen from the figures, though it is easier to understand the matter either with the aid of a heart bought from the butcher, or by means of the actual model.

The movements of the heart are automatic. If we kill a frog and open up his chest we can see his heart beating away inside the pericardium. If we remove this sac we can get at the heart itself and tie a thread on to its tip and connect the thread to a light lever, and so write a record of its movements on a smoked drum (fig. 29). We may go further. We may cut the heart completely out and connect

it to a glass tube filled with salt solution, and it will go on working and pumping the salt water for hours and hours (fig. 30). It requires a little oxygen, and it demands that the water shall contain salts

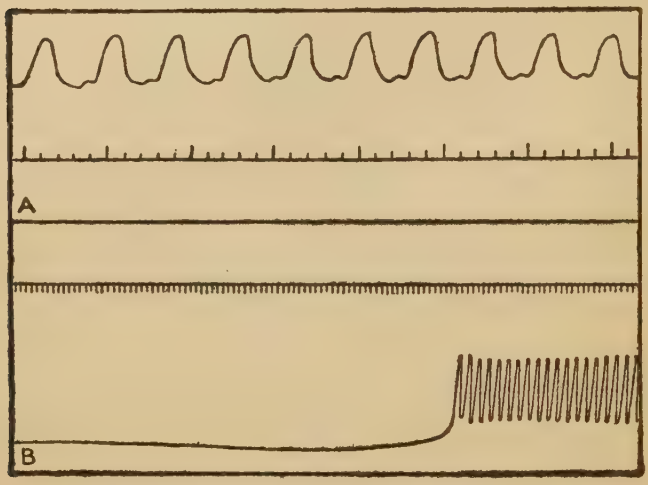


FIG. 29.—Records of the contractions of a frog's heart. The upper record shows the beat of the auricle (small rise), as well as of the ventricle (large rise). The lower record shows the immediate stoppage which results from stimulating the vagus nerve. Both records run from right to left. The drum was going much slower in the lower one (After Pembrey and Leonard Hill).

in the right concentrations and the right proportions. If these simple needs are met the little pump can go on working once a second or so for days. We may go further still. We may cut the heart up into strips and bathe each strip in the salt water, and it will go on contracting automatically for long periods and writing its record by a lever on a smoked surface. The heart has an intrinsic rhythm of its own. Its nature is to beat and to beat continuously;

it provides, so to speak, its own stimulus and does not require one from outside.

The speed at which a heart beats depends upon many factors. Each portion of the heart has a rhythm of its own. The speed, however, of the

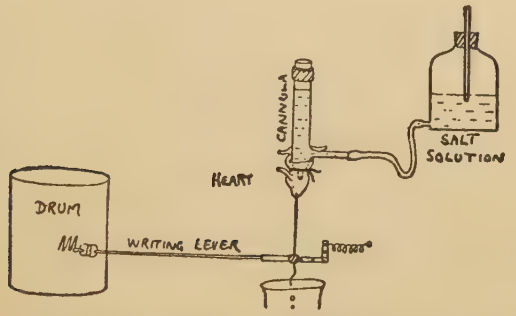


FIG. 30.—The heart of a frog, removed—while still beating—from the dead animal, tied to a cannula, and perfused with a salt solution containing oxygen, which passes out at the aorta as the heart beats (Anrep and Harris).

heart as a whole is set by that of its quickest part; for when once any portion of the heart has started a beat, the beat spreads rapidly over its surface, all the other parts following suit. The most quickly beating portion of the heart is that around the entrance of the great veins into the right auricle. Under ordinary conditions it is this part of the heart which acts as "pacemaker," the beat spreading out from there to every corner of it. It is possible, however, experimentally, and Nature had made the same experiment in disease, to hinder the free conduction of the beat over the heart. In a condition called "heart-block," which may be partial or total,

the beat does not spread completely over the whole heart. In such cases we may find the ventricle beating in its own intrinsic rhythm, much slower than the auricle. This condition is found in man (excessive smoking may be one of its causes), and it can easily be produced by injury in the case of an isolated heart.

In normal healthy animals the speed of the heart is fairly constant during rest, but rises two to four times during muscular activity. In healthy men at rest the rate of the heart-beat may be from 45 to 90 per minute, and during severe effort it may rise rapidly to as much in 180; beyond that in health, it seems unable to go, though in certain heart affections it reaches higher frequencies still. In athletic people, and particularly in athletes in training, the rate at which it beats is usually low. Ordinary people have a rate of about 65 to 75 per minute, but an athletic individual, who keeps himself fit, may get down as low as 45 or less when he is at rest, and such rates as 55 are common. As we shall see in a later lecture, the capacity of the body for hard exercise, especially when long continued, depends mainly upon the ability of the heart to meet the demand of the muscles for blood. The big and powerful heart seems to beat more slowly than the ordinary and less muscular one, and obviously if a heart beats only 45 times a minute it has a fourfold accommodation when its

rate can rise to 180, whereas if its resting speed is 90 it has only a twofold accommodation under the same conditions. Examine your friends and see if in general the most athletic have not the slowest hearts. Individual exceptions will be found, but there is no doubt of the general proposition.

The heart is governed by two nerves. These nerves do not *cause* the beat of the heart, but they are capable of influencing its rate and affecting its strength. The vagus nerve, coming from the brain (this is an "involuntary" nerve, not under our direct control), can slow the beat so much that if it is fully stimulated the heart will stop completely. A beautiful experiment can be made with an eel: his brain is destroyed, his vagus nerve dissected out, and his heart-beat recorded. Directly the coil which stimulates the nerve is started the heart stops dead and continues completely at rest until the stimulation ends: then it begins immediately to beat again (see fig. 29 for such an experiment on a frog). The other nerve going to the heart is the "sympathetic." When this is stimulated the beat becomes stronger and more rapid. In ordinary life there is a certain amount of "vagus tone," as it is called, the vagus being constantly and slightly at work, keeping the heart-rate down. As soon as exercise begins the vagus effect is removed automatically by the nervous system, and the heart-rate quickens; then the sym-

pathetic nerve comes into play, also automatically, and drives the rate still higher. If the heart-beat is recorded electrically, its rate can be seen rushing up right from the moment when exercise begins. The very first beat after the word "go" is quicker than the previous one, and within half a minute or so the rate has nearly reached its maximum value.

Excitement and emotion influence the rate of the heart. Some of us know how our heart-rate rushes up when we are suddenly called upon to make an after-dinner speech. The immediate effect is due to the nervous influences described. Another reason for the continued high rate, under conditions of excitement, is the presence of a substance, adrenalin, in the blood. Near the kidneys is a pair of glands known as the suprarenals. These produce a chemical body called "adrenalin"[1] (which the chemists are now able to make in the laboratory) which has all kinds of astonishing effects upon the body. In general it has the same result as stimulation of the so-called "sympathetic nerves": an overdose of adrenalin may give an animal, or man, many of the subjective feelings, as well as the objective appearance, of terror or excitement. During emotion adrenalin is produced by these glands and thrown into the blood-stream, and one of its effects is to

[1] Sometimes called "epinephrin" or "adrenin."

act upon the heart and quicken its rate and strengthen its beat. The anxiety of an athlete before a race is an accompaniment of the adrenalin which has been liberated in preparation for the effort. In an animal which has to fight for its life a powerful heart-beat is an important means to success, and the excitement and emotion of the struggle, or of preparation for it, cause the liberation of this substance adrenalin, which, among other effects, has the result of stimulating the heart to greater activity. To make an after-dinner speech is not perhaps as bad as to fight for one's life; but anxiety and emotion—to what-ever due—have the same bodily effect as the excitement and terror of a struggle for existence.

In the isolated heart, and in the heart of a cold-blooded animal inside its body, the rate can be affected by the temperature. A rise of temperature of 10° C. will double, or more than double, the rate of beat; a fall of temperature will correspondingly slow it. Many chemical agencies have the same effect. Absence of certain salts from the fluid in which a heart is bathed may stop it altogether, or cause it to give a very imperfect beat.

The rate of beat of the heart varies enormously from one animal to another. It is not known what it is in a whale, but it must be very low; it would be an interesting scientific adventure to try to find

out; in an elephant [1] it has been found in one experiment to be about 40 beats per minute, though this is probably far above the average: in horses at rest it is said to be about 28. In smaller animals the rate is higher. Most people have felt the rapid beat of a dog's heart; a rabbit's heart goes still more quickly; the heart of a mouse or of a little bird goes hundreds of times a minute, so rapidly that you cannot possibly follow it. The only way in which it can be counted in a very small creature, such as a mouse, is by connecting the animal to the electrical apparatus shown in Plates XI, *b* and XII. If you could look at it, such a heart, to the unaided eye, would not give any definite appearance of beating; it would show merely a rapid shiver which the eye would be unable to analyse. Only by electric means, or by a high-speed kinematograph, can the actual beats be registered.

The discovery of the circulation of the blood was made by William Harvey, who was born in 1578 and died in 1657. His work was the starting-point

[1] The elephant referred to in Lecture II, which was visiting the Children's Hospital at the Harvard Medical School, had an electrode applied to each axilla: these were held in position by two men, each wearing a rubber glove to insulate them. The beating of the animal's heart produced electric currents which were carried by wires into the laboratory and recorded on moving photographic paper. His heart-beat showed the same characteristics as those of a man, and the interval between successive beats was $1\frac{1}{2}$ seconds. This is short for so large an animal, but he may have been excited by the rather unusual procedure!

of researches which are still going on, and many of the greatest physiologists of to-day are occupied in studying the nature of the heart-beat and the factors which control the circulation of the blood. In a sense we are still only at the beginning of our knowledge of the subject. Recent work has made clear indeed many of the general laws that govern the behaviour of the heart and circulation, but we remain in ignorance of the fundamental nature of the mechanism of the cardiac muscle-cells, of their rhythm, of the mode of action of the nerves upon them, of the conduction of their contraction wave, and of the electric changes which are so easily detected when a heart beats. Professor Starling and his colleagues have described the way in which the heart adapts itself to the various loads that are put upon it during exercise. When it receives more blood to pump, its fibres lengthen and it gives a stronger beat; in consequence it requires more energy and oxygen, so the blood-vessels in the heart muscle itself open out to allow it to receive a more plentiful supply of blood. Its powers of adaptation depend partly upon the intrinsic properties of the muscle-cells themselves, partly upon a beautiful automatic mechanism of reflex nerve control, by which messages pass to the brain from heart and blood-vessels, and back from the brain to these again. Professor Starling rightly spoke in a Harveian Oration of "The

Wisdom of the Heart." The heart is indeed wise: it is difficult to imagine any way (with the material it has at its disposal, and the needs it must satisfy) in which its working could be bettered.

The left chamber of the heart pumps blood, which it receives from the lungs, into the aorta and thence around the body. A portion of this blood passes straight into the coronary artery, which opens out into the heart muscle itself and supplies it with the food and oxygen it needs. Differences between different people in their capacity for long-continued hard exercise depend largely upon differences in the powers of their hearts, and these in their turn may be due to differences in the supply of blood to the heart muscle itself. Unfortunately it is not easy to think of any way of studying and observing the coronary circulation in man. If it could be done much might be learnt about the physiology of strenuous muscular exertion.

The pressure in the arteries is relatively high: if we were to insert a long vertical tube into one of them the blood would rush up it to a height of about 6 feet, and we should see it oscillating in the tube a distance of a foot or more. As we trace the arteries out we find that they break up into smaller and smaller tubes, until finally they reach the tissues themselves which require the blood; there they branch into the minute capillaries, where the blood

corpuscles can pass only one abreast. The red corpuscles of the blood of man are only about $\frac{3}{10000}$ of an inch across, and they contain inside them a substance, hæmoglobin, which gives the red colour to the blood and carries the oxygen which the organs of the body need. Professor Krogh, of Copenhagen, has made, through a microscope, a beautiful kinematograph film of the blood-flow through these little blood-vessels. In it one can see them branching and the corpuscles hurtling through, and the way in which the capillaries join together again to form the venules, which gradually become veins and return the blood to the heart.

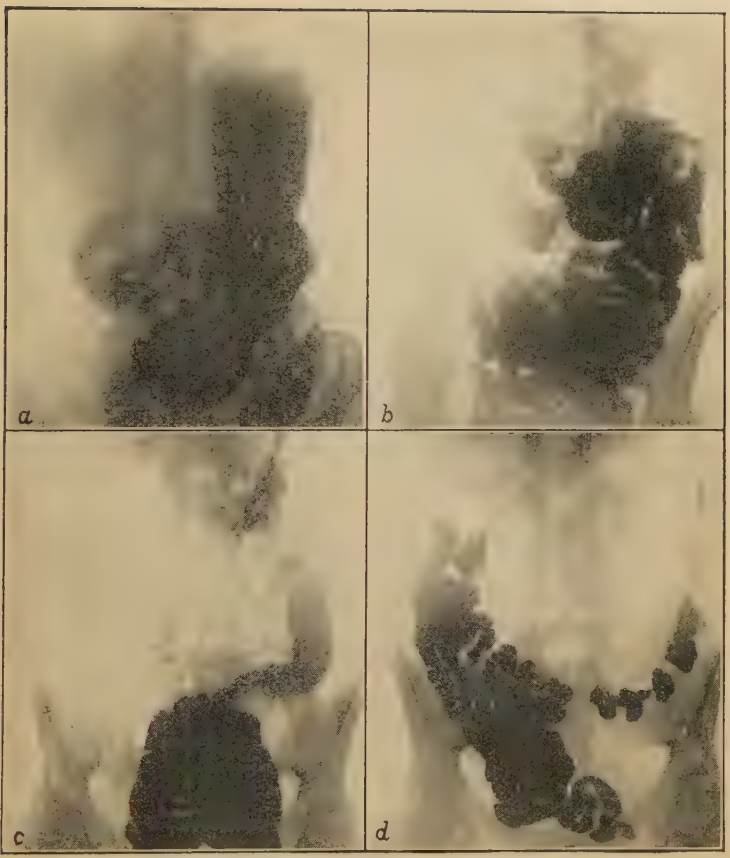
On its right side the heart receives the blood, now depleted of oxygen, from the great veins. These enter the right auricle and pass into the right ventricle, which (when the heart beats) forces the blood out into the pulmonary artery, from which it travels by branching blood-vessels, getting ever smaller and smaller, till it finally passes through the lung capillaries; these are spread out all over the surface of the lungs. The lungs consist of millions of little bags, which are filled with air and emptied again as we breathe, and the blood in the capillaries is brought into close contact with this air; from it the red corpuscles take oxygen, and to it the blood surrenders carbonic acid. Thus, the air which comes out again from the lungs has lost some of its oxygen and has

gained carbonic acid. We shall hear more about this in the next lecture. After passing the capillaries of the lungs the blood is gradually gathered together into veins, and finishes up in the pulmonary vein, from which it pours once more into the left side of the heart. There it begins its circuit again.

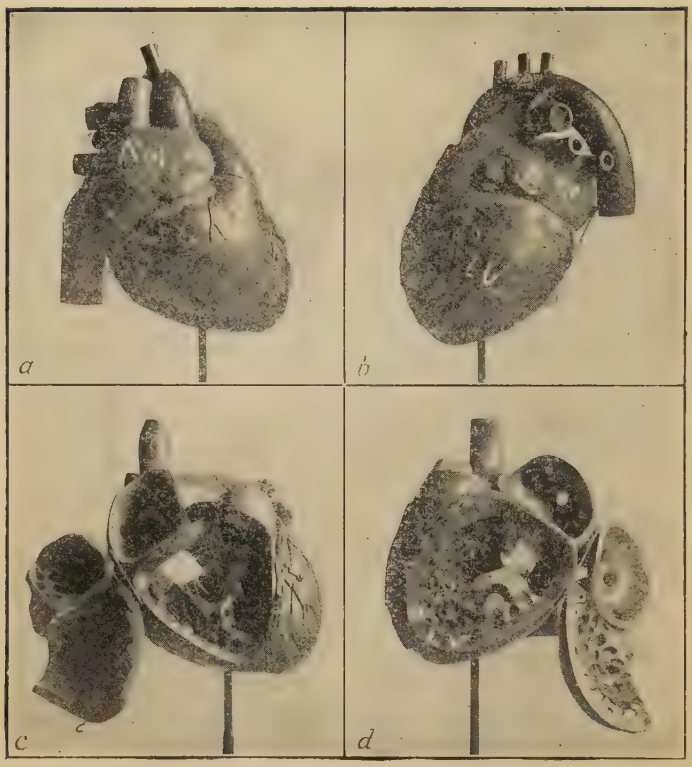
The heart is perhaps the most important organ in the body, because the effect of its going wrong is so immediately disastrous. Consequently from the earliest days people have devoted much time and trouble to studying it, and there are many ways in which its movements and behaviour can be observed. I have spoken already of what can be done with the isolated heart. Let us consider now how we can observe the heart in a healthy normal animal,—for example, in man.

An obvious way is that of feeling the pulse. When the heart beats it sends out a mass of blood, about a quarter of a pint, into the aorta. The arteries are elastic, and when this mass of blood is suddenly forced into them they expand and a pulse of pressure runs along them (fig. 31). The flow of blood itself is almost continuous; it rises and falls a little at each beat, but owing to the elasticity of the arteries it runs, throughout the cycle of the heart, at a practically constant speed.

The pulse is not a *flow* of blood—it is a *wave* of pressure. It runs along the arteries fairly fast—



X-ray pictures showing stomach and intestine after an opaque meal. (*a*) Immediately after. (*b*) Two hours after. (*c*) Three hours after. (*d*) Seven hours after. The changes between the successive exposures are due to the activity of the involuntary muscles propelling the food along the digestive tract (p. 87).



Models of the heart. (*a*) Right side, showing superior (SVC) and inferior (IVC) venæ cavæ, right auricle (RA), aorta (A), pulmonary artery (PA), and pulmonary veins. (*b*) Left side, showing left ventricle (LV), left auricle (LA). (*c*) Same as (*a*) but opened to show valves and interior of right heart. (*d*) Same as (*b*) but opened to show valves and interior of left heart (p. 94).

much faster than the blood itself. In man it varies in speed at different times of life and with different conditions of the vessels; in a child it runs 4 or 5 yards a second. The more rigid the arteries are,

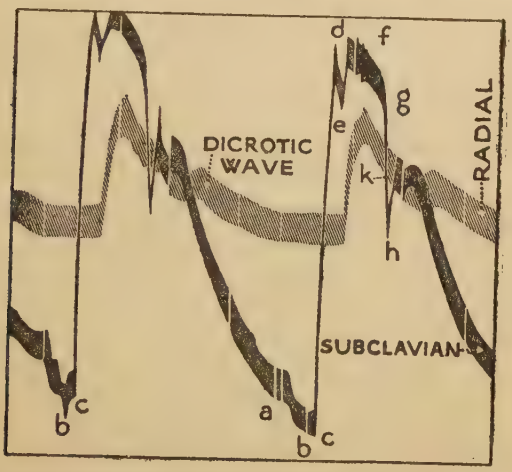


FIG. 31.—Records of pulse-wave taken simultaneously at two different points—the radial artery (in the wrist) and the subclavian artery (near the collar-bone). Note the beat of the auricles between *a* and *b*; the sudden rise of pressure at *c*, when the blood first pours into the arteries; the fall at *g*, when the heart begins to relax; and the sudden closure of the valves at *h*. Note also that the wave reaches the subclavian artery, which is nearer to the heart, sooner than it reaches the radial artery (Wiggers).

the more rapidly the pulse-wave runs, so that a measurement of the pulse-wave velocity tells us directly the condition of the arteries. There is a simple formula for this:

$$V = \frac{3 \cdot 57}{\sqrt{\text{percentage increase in volume of artery per mm. of mercury increase of pressure,}}}$$

where V, the velocity, is measured in metres per second. It is possible to measure this velocity fairly

accurately. We place a receiver on the carotid artery in the neck and another on the radial artery in the wrist. The wave starts off from the heart and reaches the neck earlier than the wrist; the time interval can be measured, and the distance between the two places read off on a tape-measure. From this we can determine the velocity of the pulse-wave, and so can calculate the elasticity of the arteries. The more elastic they are, the better for their owner: they lose their elasticity as he grows old.

The form of the pulse-wave tells us a good deal about the heart. It can be registered very simply by placing a "sphygmograph" over the artery and allowing the pulsations of the latter to work a lever which writes upon a moving strip of paper. Better and more accurate, though more complicated, is the employment of photographic registration (as in fig. 31) by means of a beam of light reflected from a little mirror on a tambour, which is moved by the pulsations of the artery. From such records abnormalities may be detected in the valves of the heart, or in the conduction of its beat.

Another somewhat similar way is to replace touch, or sight, by hearing, and to *listen* to the pulsations of the beat, and much may be learnt about the condition of the heart and its valves, either by putting the ear directly to the chest of a subject, or by bringing the sounds to the ears (which is more

convenient) by means of a stethoscope. The ear of a trained physician is a wonderful instrument for this purpose, though even the inexpert can recognise two of the sounds of the heart. When the heart muscle contracts there is a low-pitched roar, which generations of medical students have heard described as

LUBB.

When the heart muscle relaxes the blood rushes back and would fill the heart again were it not for the valves, which promptly close with a sharp and high-pitched

DUP.

This lubb, dup—pause—lubb, dup—pause—can be picked up by a microphone, and amplified by valves till the sound of a man's heart can be heard all round a hall. It might even be broadcast on the radio so that physicians all over the country would be able to diagnose its condition!

Then the blood-pressure can be recorded (fig. 32). A rubber bag is strapped round the soft part of the upper arm and blown up with a pump, the pressure being recorded on a gauge or mercury column; when the pressure in it is high enough it squashes the arteries flat, and the pulsations from the heart cease to get through to the lower part of the arm. We may feel with our fingers for the pulsations on the far side of the bag, or we may listen with a steth-

oscope. In this way we can ascertain the highest and the lowest pressures that occur in each individual beat.

Another way in which the heart can be studied is by means of the electro-cardiograph. About

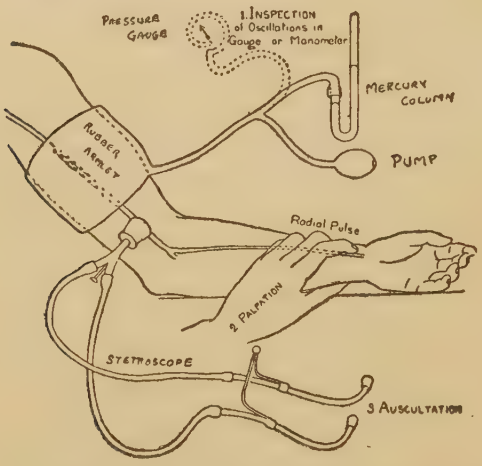


Fig. 32.—Method of finding the blood-pressure in man (Anrep and Harris).

twenty years ago Professor Waller showed in London, at a conversazione of the Royal Society, the heart-beat of his dog recorded by a capillary electrometer. The anti-vivisectionists protested against what they imagined were the tortures inflicted on the dog, and questions were asked in the House of Commons. The Home Secretary replied that if his "honourable friends had ever paddled in the sea they would know the sensation" experienced by the subject of the experiment. That indeed is the case. If a dog

stands (it is not difficult to teach him the trick) with his two feet in separate bowls of salt water, the electric currents produced by his heart can be led off from the bowls by electric wires to the instrument and so exhibited to an audience (Plate XII, *b*). It had long been known that when a heart beats, just as when a muscle contracts, an electric change passes over it. In an exposed or isolated heart these electric currents can be recorded by placing electrodes directly on the heart and so leading the current away. This method has provided much useful information about the path of the wave that travels along a heart when it beats, but it was obviously not applicable to man, in whom the heart certainly cannot have instruments placed directly on it. These electric currents, however, are so strong that Waller found it to be unnecessary to expose the heart itself, indeed almost any two parts of the body will act as suitable electrodes. The best two leads are the right arm and the left foot, but good records are obtained from the two arms, merely by placing the two hands in bowls of salt water and leading the current away to the galvanometer.

More recently Professor Einthoven, of Leyden, has invented the string galvanometer (Plate XI, *b*), by which these currents can be very readily detected. This instrument consists in principle merely of a strong electro-magnet with a very fine conducting

wire passing between its poles. If an electric current runs down the wire it is deflected to one side in the

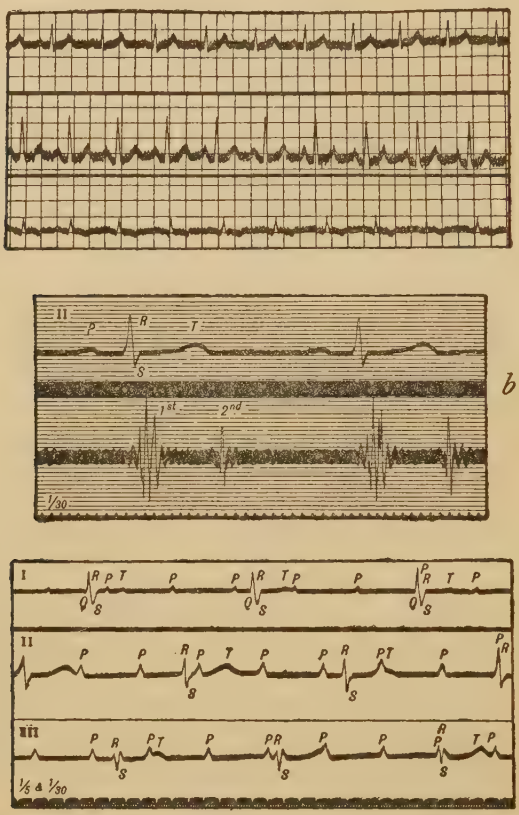


Fig. 33.—Records of the electric currents produced by a human heart while beating ("Electro-cardiograms"): (*a*) taken over telephone lines; (*b*) with simultaneous record of heart sounds ("phono-cardiogram"); (*c*) of a case of complete heart-block. In (*a*) and (*c*) three records are given; in the uppermost the currents were led off from right hand and left hand of the subject; in the middle one from right hand and left foot; in the bottom one, from left hand and left foot. (Cambridge Instrument Company.)

magnetic field, and by means of powerful magnification through a microscope an enlarged image of

the wire can be thrown on a screen and its movements seen, or recorded on a falling photographic plate. The subject places his (or her, see Plate XII, *a*) hands in bowls of water, the operator opens a switch, and the movements of the heart, or rather the electric waves accompanying them, are made visible at once. Fig. 33 shows typical records made by the string galvanometer. The first record (Fig. 33, *a*) is of the currents produced by the heart of a patient at Addenbroke's Hospital, Cambridge, England, taken over ordinary telephone lines to the Pathological Laboratory nearly half a mile away, and there recorded. The second record (Fig. 33, *b*) is a normal "electro-cardiogram" accompanied by a "phono-cardiogram," the electric current produced by the heart being the upper of the two curves, the sounds (picked up by a microphone) being the lower. P is the beat of the auricles, RS that of the ventricles, T represents the onset of "diastole" as the beat passes off. The third record (Fig. 33, *c*) is of a patient suffering from complete "heart-block," the auricles (P) beating in their own rhythm, and the ventricles (RS) independently in theirs.

The string galvanometer is a wonderful instrument, and much has been learnt by it concerning the conduction of the wave of excitation in the heart. By its means, at the hands of Sir Thomas

Lewis in London, working upon dogs and men, some of the most grievous disorders of the human heart have been explained and their treatment improved. It has been used, however, for many other purposes. It was employed for sound-ranging in the War, and to-day Professor Einthoven and his son are developing a new type of it, by which wireless-

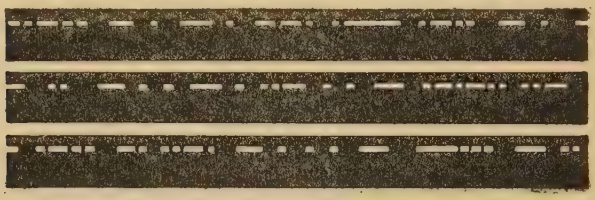


FIG. 34.—Wireless-signals from the Dutch East Indies picked up and recorded photographically in Holland by a string galvanometer. When the signal is going, the currents set up by the waves cause the string to oscillate and the line becomes wide and blurred: when the signal stops the string ceases to vibrate and the record becomes narrow and clear again. The string is very short and fine, and works in a high vacuum (Einthoven).

signals from the Dutch East Indies can be recorded in Holland on a moving photographic strip (see fig. 34). It is impossible to know where scientific progress will lead. No one could have expected that a study of the conduction of electricity through gases, leading to the discovery of X-rays, would have enabled us, as we shall hear in a moment, to see with our own eyes the beating of the human heart; nor could it have been imagined that the labours of the physiologists who studied years ago the mechanism of the heart-beat in frogs and turtles would have led to the location of enemy guns on the French battlefields,

or to recording wireless-signals from the Far East. Such things show that there are no watertight compartments in science, that no one can tell where progress may come from, and that we need always to keep our eyes wide open to see whether something that someone else has discovered or invented, in quite another job, often in another country, may not be of the greatest importance to us in ours.

I mentioned the use of X-rays for studying the movements of the human heart. The more solid parts of the body stop X-rays, and so cast a shadow on a photographic plate or upon a screen coated with fluorescent material. Bones stop X-rays much more effectively than anything else in the body, but a thick solid muscle like the heart, or the diaphragm, possesses a certain stopping power, especially for the softer rays, and so a shadow of the heart and diaphragm can be cast on a screen. If the apparatus employed be very powerful it is possible practically to take "snapshots" of the heart of a subject standing up in front of a photographic plate; or by placing a piece of paper against the screen to draw in an outline of the heart in one particular phase of its cycle, and so to measure it up. Thus we can find whether it is normal in size and position, to some degree we can observe its movements.

Plate XI, *c* shows an X-ray "snapshot" ($\frac{1}{8}$ sec. exposure) of the chest of a girl fourteen years old. This also is a negative of the original exposure, showing dark the parts of the body that cast a shadow on the plate; the bones and vertebræ, the jaw, skull, and teeth are obvious enough. The two large light spaces are the lungs. In the middle, crossing the vertebral column, but lying somewhat on the left of the child (on the right looking at the picture) is the heart, resting on the diaphragm muscle beneath it and tipping over towards the left side of the body. Plate XI, *c* is practically an instantaneous photograph of the heart. Even more rapid ones can be taken, for example, in $\frac{1}{100}$ of a second, and with such short exposures a perfectly clear, sharp outline can be recorded. The heart is moving very rapidly, and nothing but very short exposures give a really clear edge, suitable for measurement. For demonstration purposes it is perhaps more convincing to allow one's audience to observe the same thing directly for themselves on a screen, with a living subject standing in front of it. Then the beats of the heart, its changes of position and volume during its contractions, can be plainly seen. So also can the movements of respiration: as the subject breathes the diaphragm muscle on which the heart rests moves up and down—down for inspiration, up for expiration,—so that the apparatus for

breathing, as well as that for circulating the blood, can be observed with the naked eye on a screen. It is even possible in this way to measure up the size of the heart and to get an approximate idea of how much smaller it is at the height of its contraction than at the height of its relaxation, which determines how much blood it gives out in every beat.

It is strange and interesting to reflect that Plate XI, *c* could never have been made if physicists had not studied the conduction of electricity through gases, of which X-rays were a side product. Imagine fifty years ago a prize offered to anyone who could photograph the inside of the body in a living child. He and any who tried to win the prize would only have been laughed at for their pains. Certainly those who set out to win it would have been most unlikely to succeed. Success came from a totally different direction, from the work of men who to their severely practical brothers may have seemed to be investigating things of little importance. Often in science, as in life, it is the by-products which turn out in the end to be more important than the things we set out to find. Amplifying valves and X-rays and radio are just such by-products. One never knows where scientific investigations will lead, but experience has made it certain that a disinterested and honest study of nature, an attempt to under-

stand the real facts behind the shadow, will lead at intervals to discoveries of the first importance for the comfort and well-being, mental, moral, and material, of the race.

LECTURE IV

The Lungs and Blood. How the Muscles get Air and Fuel

All machines require energy in order to supply mechanical work, which is a form of energy. All the ordinary machines with which work is done get their energy directly, or indirectly, by burning fuel. The steam-engine employs coal, wood, or oil to boil water, the steam driving a piston in a cylinder, or else twisting a turbine by blowing at high speed on its blades. The gas-engine, the oil-engine, and the gasoline-engine produce a high pressure by an explosion, which also drives a piston down a cylinder. An electric motor is driven by an electric current, but this current is being made by a dynamo which is driven by another engine which uses fuel in the same way. Even if the electric motor is driven off accumulators, these are charged by an electric current which is made in the first instance by the energy obtained from the burning of coal or oil. Other types of machines are of course possible: for example, the heat of the sunlight can evaporate water which can raise a piston, or it can heat the air, which is set in motion, producing winds, which then can be harnessed by windmills to do work. The evaporation

of moisture by the sun produces clouds and rain, which are the cause of rivers; and these rivers can turn watermills, or water turbines, and so provide us with mechanical energy. Or again, we can make an electric battery—for example, of copper, zinc, and sulphuric acid—which will provide an electric current and turn an electric motor. It is not *necessary* that the energy required for a machine should come from the combustion of fuel; it may, as we see, come from other things. All the machines,[1] however, which are used on a large scale for commercial and industrial work are of the nature of combustion engines, in which fuel is combined with the oxygen of the atmosphere to form carbonic acid and water with the liberation of energy. The same thing is true of muscles, which obtain the whole of the energy they require from the burning of the foodstuffs which we eat. In considering, therefore, the activities of muscle, it is obvious that the most important thing is the means by which fuel and oxygen are supplied.

It used to be imagined that the oxygen, which is taken into the lungs by the movements of respiration, was employed there in order to burn substances which are brought to the lungs by the blood. This idea is wrong. When the lungs are expanded by the action of the diaphragm and the other respiratory

[1] Apart from those employing water-power.

muscles, air pours into them down the "bronchi," which break up gradually into smaller air-passages, until finally they reach the smallest "bronchioles." From these the air flows into the "respiratory bronchioles," the "alveolar ducts," the "atria," and the "air-sacs." (Fig. 35.) These air-sacs are cavities of which the walls are composed of "alveoli" or air-cells. The alveoli are covered with a network of fine blood capillaries (fig. 36), through which the blood rushes, picking up oxygen from the air in the air-sacs, and giving out carbonic acid as it goes by. The lungs are made up of thousands of lobules, like the three shown in fig. 35, all tightly packed together and intersected in all directions by blood-vessels. When the respiratory muscles relax, the lungs collapse under their own elasticity, and the air pours out again.

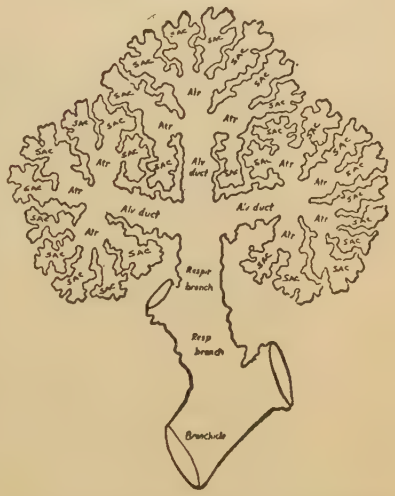


FIG. 35.—Three lobules of the lung showing bronchiole, respiratory bronchiole, alveolar ducts, atria, and air-sacs (J. S. Haldane).

Very little oxygen is used in the lungs themselves, the vast majority of it passes through the very thin

membranes which surround the alveoli (fig. 35) into the capillaries (fig. 36), through which the blood runs, and into the blood corpuscles, of which the blood is largely composed. Unfortunately for animals oxygen is a very insoluble gas. In the atmosphere about 21 per cent. is oxygen; in the lungs, owing to the fact that the gas is rapidly passing

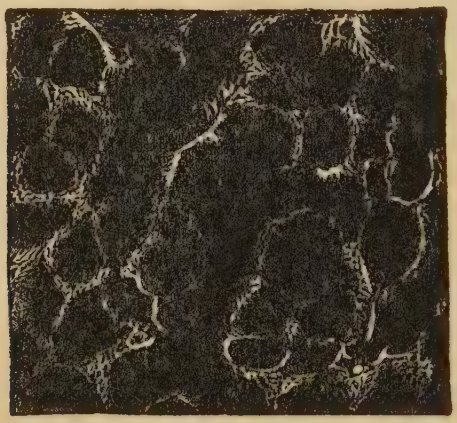
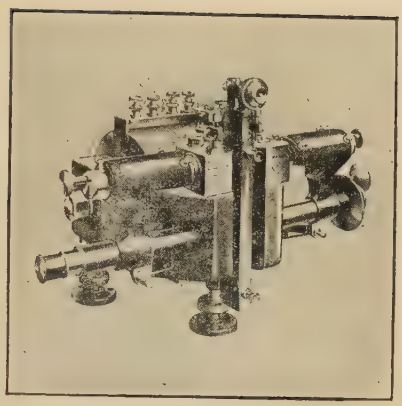


FIG. 36.—Network of blood capillaries in the human lung—a section across a lobule such as shown in fig. 35. The surface of each air-sac is thickly covered with the finest blood capillaries, through which the corpuscles rush in single line, one after the other (Kölliker).

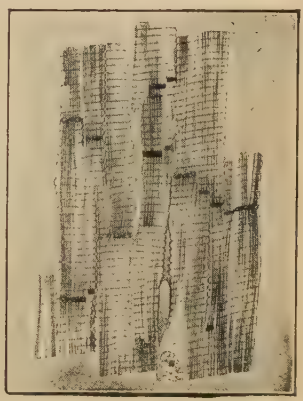
away into the blood, only about 17 per cent. If we had no red corpuscles in our blood—actually we each have about 25,000,000,000,000 of them—it would require about 300 gallons of blood to carry 1 gallon of oxygen. Since a man rowing in a crew may want about $1\frac{1}{4}$ gallons ($4\frac{1}{2}$ litres) of oxygen every minute, his heart would have to pump round about 375 gallons of blood every minute to supply

(*a*) Microscopic appearance of muscle-cells of intestine (× 530). The fibres have no tendons and are fitted or inlaid into a sheet. Each cell has a "nucleus," shown dark, which is concerned with its growth and the maintenance of its condition (p. 86).

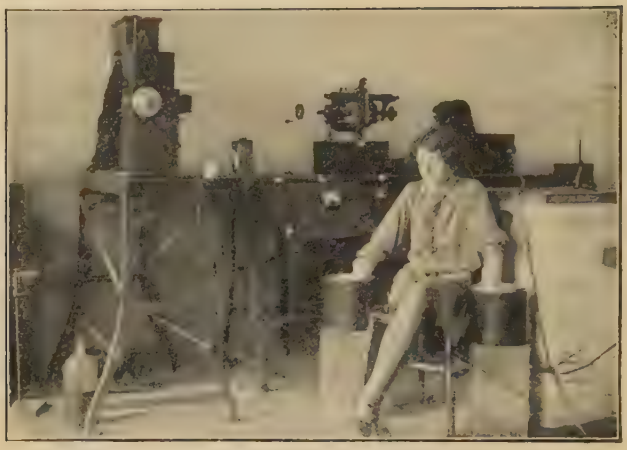


(*b*) String galvanometer invented by Professor Einthoven of Leyden (pp. 50, 102, 111).

(*c*) An X-ray snapshot ($\frac{1}{8}$th second) of the chest of a girl of fourteen, showing the lungs, heart, and diaphragm beneath it (pp. 94, 116).



(*d*) Fragment of human heart muscle (× 2300). In the heart the fibres occur in short blocks, not in long threads as in voluntary muscle (p. 91).



(*a*) String galvanometer ("electrocardiograph") as used for recording currents produced by the human heart. Note galvanometer with microscope, lamp for illuminating the string, camera, and electrode vessels leading electric currents produced by the heart to the galvanometer (pp. 102, 113).

(*b*) Dog standing in two pots of salt water, from which the electric currents produced by its heart are led off along the wires (p. 111).

him with the oxygen he requires. The total amount of blood in the body of a 170 pound man is only about $1\frac{1}{2}$ gallons, so that his blood would have to rush round 250 times every minute—about 4 times every second—had he no corpuscles to help him carry the oxygen. Such a state of affairs would of course be entirely impossible; no heart, however large and strong, could cope with anything like this amount of fluid. The difficulty has been got over by a method which is common to all animals except the very smallest (which can get their oxygen by direct diffusion from the outside). That method involves the use of hæmoglobin (or of some related substance [1]), the red pigment of the blood, which can combine chemically with oxygen and so carry it in much larger quantities than could ever exist in simple solution.

Throughout the whole of Nature, in almost every living cell, there is found a substance called "cytochrome"; it is not there in large amounts, but it can be recognised by its colour and spectrum. Cytochrome contains an atom of iron attached to a fairly complicated chemical substance. It seems to be concerned with the actual mechanism by which

[1] For example, in crabs and lobsters the blood contains hæmocyanin, a pigment built up round an atom of copper, which turns blue when it combines with oxygen, and colourless when it gives up the oxygen again. There are no corpuscles in these creatures' blood: the hæmocyanin occurs simply in solution.

oxygen is used by the living cell. It is capable of combining with oxygen and of releasing it again. Allied to this, and probably built up from it by Nature during the long process of trial and error which has taken place in Evolution, is the substance hæmoglobin, which in some of the lower animals occurs in solution in the blood, but in the higher animals exists in very concentrated solution inside the blood corpuscles. In man these corpuscles are little circular discs, made up of a delicate elastic envelope with the hæmoglobin inside. They are easily bent, which allows them the more readily to pass through the narrow blood capillaries. They are about $\frac{1}{3000}$ of an inch across, and about $\frac{1}{12000}$ of an inch thick. The hæmoglobin which they contain is present in the blood in very large amounts. It is, as is cytochrome, a compound of iron, and each molecule of it, containing one atom of iron, is able to combine with one molecule—that is, with two atoms—of oxygen. The quantity of it in the blood differs in different people. In ordinary men the amount is such that every 100 volumes of blood can carry, combined with hæmoglobin, about 20 volumes of oxygen. In people who have become acclimatised to high altitudes—for example, by living at 15,000 feet in the Andes or Tibet,—there is considerably more hæmoglobin, and the blood can carry correspondingly more oxygen. In anæmic people the

amount of hæmoglobin is less, their blood can carry less oxygen, and they soon get breathless when they take exercise. We see now what an enormous advantage this hæmoglobin is to us. To carry 1 gallon of oxygen the amount of blood required is only about 5 gallons instead of the 300 which would be needed were there no hæmoglobin in it. Thus, if the muscles of a man were capable of taking all the oxygen out of the blood every time it went round, a runner requiring 1 gallon of oxygen per minute would only need to circulate 5 gallons of blood round his body in that time. Actually the muscles cannot take out all the oxygen from the blood as it goes rushing through them, there is still some left in it when it returns to the lungs. In order, however, to get 1 gallon of oxygen it is not necessary to circulate more than about 7 gallons of blood, which is less than one-fortieth part of the amount that would be required were there no hæmoglobin present. Seven gallons to circulate in a minute is still a heavy task for the heart, but it is a possible one if the heart is strong and good, so the needs of the body can be met. Were it not for the hæmoglobin in our blood, even with the most frantic efforts that the heart could make we could not get more than one-half to one-third of the oxygen we need, even while we remained as quiet as possible in bed!

It has been calculated that if all the little air-sacs

of the lung could be laid out flat and measured up they would occupy a surface, in an ordinary man, of about 100 square yards, about equal to the area of the walls and ceiling of a fairly large sitting-room. The blood has to be very well mixed with air in order to allow it to take up the oxygen which is needed by the muscles, and give out the carbonic acid which they have made. If the lungs were not big enough the blood would have to rush through the capillaries so fast that it would not have time to collect the oxygen on its journey, and it would return to the muscles without its full complement of that gas. Thus a good large pair of lungs is a necessity to anyone who is to take hard exercise for a long time, and it is found that in people accustomed to heavy work, especially in athletes such as runners, oarsmen, and swimmers, the lungs tend to be large. The effective size of the lungs can be measured in a simple way by the use of a gas-meter (Plate XVI, *a*). The subject takes as deep a breath as he can and then blows it all out, to the last gasp, through the meter, and the volume expired is read. The result is called the "vital capacity," which in a powerful athletic man may be 5 litres (rather more than a gallon) or more, and which in ordinary people varies from 2 to 4 litres. In a certain runner, the winner of many Marathon races, who weighs only 130 pounds, it is as high as 5.4 litres: an astonishing

value for so relatively small a man. Like a slow heart, you will almost invariably find a large vital capacity in an athlete, and though one cannot lay down any rule about it that will always hold, you will notice that healthy outdoor people usually have a larger one than less vigorous and indoor people. It is an amusing exercise to make a series of measurements on one's friends and to invite them to have competitions with one another. Of course you must realise that there is still a fair amount of air in the lungs when the deepest expiration has been made, but this amount is roughly proportional to the vital capacity, so that the latter gives us a good idea of the working size of the lungs.

There is another factor in connection with the lungs which is much more difficult to measure. The ease with which oxygen passes from the air-sacs into the blood depends not only upon the area of the lung wall and the degree to which the lung is ventilated, but also upon the ease with which the oxygen passes through its membrane. This process depends upon what is known as "diffusion." Diffusion is a purely physical process—the slow and gradual mixing of two gases or two fluids, or one gas and one fluid—which is due to the perpetual motions of the molecules that make them up. Recent work by Professor Barcroft of Cambridge, England, and his colleagues in America has strongly suggested that those people

who suffer from mountain-sickness at high altitudes are also those who possess a poor "diffusion constant" of oxygen through their lung membranes, while those that do not suffer so much have a high one. Probably if the diffusion constant could be studied in the greatest long-distance athletes (and there is no reason why it should not, if they would come and let physiologists experiment upon them) we should find that they also have lung membranes which very readily let oxygen through. Thus for athletic power, as well as for standing high altitudes without distress, large lungs with a good "ventilation" are needed, and also those more subtle and less easily measured qualities which permit the oxygen readily to pass through into the blood.

Once the oxygen has got through the lungs it is carried round at fairly high speed through the arteries till it comes to the minute capillaries, where the corpuscles pass, one by one, through narrow tubes and come in very intimate contact with the muscles which they supply. In the muscles, at any rate during work, there is what we may call an "oxygen vacuum," so that there is a big head of pressure driving oxygen from the blood into the muscles that need it. During work the number of capillaries in the active muscles, which are actually open and allowing the blood to pass, is enormously increased, so that although the volume of blood

per minute which is circulating is much greater than it is in a man at rest, it is passing no faster, probably even rather slower, through the capillaries themselves than in a resting man. Consequently there is time for it to get rid of most of its oxygen, and the blood comes to the end of the capillaries and passes into the veins and returns to the heart with only about 30 per cent. of its oxygen left. Probably from a very active muscle the amount of oxygen is less than 30 per cent. of the full amount, but we can only determine the quantity of oxygen in the *mixed* blood that returns to the heart, and a part of this blood has come from muscles and organs (*e.g.* the brain) that are not very active. The blood comes back to the right heart and passes from it round through the lungs again, back to the left heart, and from there is forced out once more into the circulation.

To understand these matters an elementary knowledge of the anatomy of the human body is necessary. Plate XIII, *a* is a photograph of a demonstration model of a man. In Plate XIII, *b* it is shown with half its head, one arm, and the front of its body removed, to exhibit its internal organs. Above we see the lungs, below them the diaphragm and liver, and below them the intestines. The parts removed are placed on a chair by its side. In Plate XIII, *c* the heart and lungs have been taken out, and placed on a chair, or in front of the model. In Plate XIII, *d*

the liver, diaphragm, stomach, spleen, and intestines have been removed. It is an amusing exercise to take such a model to bits and try to fit it together again.

In dealing with working muscles the blood has a double duty to perform: it has to carry away carbonic acid, which is produced by combustion there, as well as to bring in oxygen. This carbonic acid is carried in the blood, not directly in combination with the hæmoglobin, but in a way with which hæmoglobin has a good deal to do. The carbonic acid passes from the blood into the lungs and is found in the air which is breathed out. In the air which goes in there is practically none, in that which comes out there is about 4 per cent. If we hold our breath for a while the carbon dioxide collects in the air of the lungs, and the blood going away to the brain carries more than its proper amount of it; this stimulates what is called the "respiratory centre" in the brain, which immediately sends powerful impulses to the muscles which work the respiration, and finally we are forced to allow these to carry on. If, by artificial means, we breathe air containing a high percentage, say 3 or 4 per cent. of carbonic acid, the blood leaving the lungs will carry too much of this away, or rather it will not give up its usual amount, the respiratory centre will be excited, and the rate of respiration will be increased and its

depth exaggerated. On the other hand, if by breathing deeply in and out at a time when the muscles are not producing much carbonic acid, we forcibly get rid of a large amount of that substance, the blood passing through the respiratory centre will contain too little of it, it will become rather too alkaline, the respiratory centre will cease to work, and the muscles concerned with respiration will get no orders to contract and relax. Consequently for a long time it will be possible to hold one's breath—indeed, the best way to win a competition at holding one's breath is to precede the effort by a long period of deep breathing, and so get rid of a considerable fraction of the carbonic acid which is present in the blood. It is an easy experiment to try, but do not push it too far or the results may be rather unpleasant.

Even with the best arrangement that Nature can provide, namely, hæmoglobin, the amount of blood which must be circulated in order to supply a man with the oxygen he needs for heavy work has to be rather large. This places a considerable load on the heart, which, however, in a healthy person, it is quite well able to bear. The heart, moreover, is aided in its efforts by another important factor, namely, the movements of the body itself. The rapid movements of the muscles tend to pump the blood along in the little veins into which the capilla-

ries collect, and along the larger veins returning to the heart; these possess valves (fig. 37) pointing towards the heart, to aid these movements of the body in returning blood. The movements pump, or massage, the blood along. If a man makes a violent effort with his body still and rigid, as in lifting a heavy weight or in raising himself in a gymnasium, these movements do not occur, and blood tends to stagnate in the smaller and greater veins; it does not return to the heart as rapidly as it might, the muscles get too little oxygen and fatigue comes on rapidly. In other forms of exercise, such as running, skipping, and playing open games like tennis, the movements of the body are very rapid and help greatly in the return of blood, and so increase its rate of circulation. Some forms of exercise are intermediate, such as rowing, where the movements, although very powerful,[1] are relatively

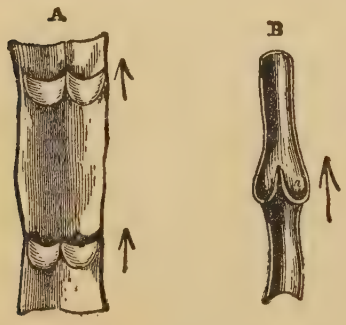


FIG. 37.—Valves in the veins which allow the blood to move towards the heart, but hinder it from pouring back into the limbs. In (A) the vein has been slit down one side to show the two opposing valves. In (B) it has been slit down the middle to show the valves closed (Halliburton).

[1] A man rowing for three or four miles in an eight-oar boat can develop over half a horse-power of mechanical work the whole way!

slow, about thirty to thirty-five strokes a minute, only one to each five or six cycles of a heart going full speed. In rowing, therefore, there is a somewhat excessive strain placed upon the heart muscle itself, though actually the greatest oxygen consumptions ever recorded have been found in oarsmen [1] rowing at high speed: the movements of the body are not rapid enough to help the heart in the circulation of the blood, and it has to do the whole job itself. Consequently in oarsmen we sometimes find over-developed hearts, and in rowing, more than in most kinds of athletics, we must keep a watch on the heart in case of trouble.

Any of the common foodstuffs can be used by the body for muscular work, and of these fat contains, per unit of weight, more than twice as much energy as any other. In the muscles themselves, however, there is evidence that the fuel directly employed is sugar, and if other substances are used by the body for doing muscular work they are probably changed by other organs of the body into sugar before they are so employed. There is, as a matter of fact, considerable dispute about this at the present time, but, in any case, it is true that the chief part of

[1] It is only fair to note that these oarsmen were very big men, and that reckoning their oxygen consumption per pound of body weight runners have far the best of it, because their movements are much easier and more frequent.

the fuel employed by muscle is sugar, even if the muscles themselves are capable of using other things. This sugar, apart from any which may be made by the liver or other organs from proteins and fat, comes from the sugar we eat in our food, but especially from the starch which is found in such things as potatoes, bread, and rice. Starch is broken down in digestion into glucose or grape-sugar, which is absorbed into the blood, and is either used directly or else is turned, in the muscles, into a substance "glycogen," which is the immediate store of fuel required for muscular work. Glycogen is found also in the liver in large amounts, and when the supply in the muscles is exhausted the liver glycogen turns into sugar again, passes into the blood, and finds its way to the muscles ready to be used by them.

Glucose is always present in the blood to the extent of about one part in a thousand. In diabetes it rises to higher concentrations, in starvation it falls. It is a very valuable substance and it possesses a considerable amount of energy. One gram of glycogen, which is built up from glucose, contains enough energy, when burnt, to warm a litre of water, about 3.8° C, enough to raise a weight of 1 ton about 6 feet into the air, enough to lift a man of 170 pounds about 70 feet. Thus the work done in raising a man straight up a distance equal to the height of the Woolworth Building in New York is equivalent

to the energy that would be supplied by burning about 11 grms.—that is, about $\frac{4}{10}$ of an ounce—of sugar or glycogen. Sugar, therefore, is a very satisfactory means of storing energy within the muscles of an animal, and, if these be examined they will be found to contain within themselves somewhere about $\frac{1}{100}$ of their weight of sugar in the form of glycogen deposited inside the muscle-cells. This they use during work: if the work is heavy the glycogen tends to get used up, and then it is restored by sugar coming from elsewhere: for example, either from the digestive tract, whence it passes to the blood by absorption, or from the liver, where it is kept in store. In starvation the muscle glycogen gradually diminishes but never disappears; all the fat in the body is gradually broken down, even the proteins of the tissues themselves may be used, but still there is a trace of glycogen left. Without it muscular movement would be impossible; and without muscular movement life would end.

Let us return now to the subject of fatigue, which we discussed in Lecture II. If the exercise is very hard, the muscles will not be able to get enough oxygen to meet their needs. As we shall hear in a later lecture, a good 100 yards runner, going at full speed, would need 30 litres or more of oxygen per minute if he were required—and able—to continue that speed for long. Actually we know that no

man's heart and lungs can supply him with more than about $\frac{1}{7}$ of that amount, so he cannot go on at such a high speed for more than a fraction of a minute, he rapidly becomes tired, he quickly acquires what we call an "oxygen debt." This tiredness is due mainly, if not entirely, to the appearance of lactic acid inside the muscle-fibres themselves. That substance, which comes from the glycogen inside the fibres, makes them acid and stiff, and when it has collected in sufficient amount they refuse to work any more. They need a rest to allow them to recuperate, and during that rest they go on using oxygen and burning sugar to provide them with the energy required for the removal of the lactic acid. In the end, when all the lactic acid has been restored, as the glycogen from which it came, the muscles have entirely recovered from their fatigue and are ready to start and do the work over again.

In ordinary people "out of training" violent exercise may leave them stiff and sore. This stiffness is such an obvious thing that one of the first questions which a physiologist is called upon by his friends to answer is, What is it due to? How can it be cured? Many a time have I had to answer that I do not know. I forestalled your questions by telling you at once of my ignorance. Physiologists are very ignorant people; perhaps it is partly their own fault, but largely, I hope you will admit, it is due to the

difficulties of the subject they study. I am sorry, but I cannot tell you what muscular stiffness is due to, though I am sure that embrocation, as such, will not cure it! Perhaps in an untrained muscle violent effort causes an actual strain or injury to the sarcolemma of the muscle-fibre; perhaps in some cases the acid which is produced in large amounts during exercise causes a sort of partial coagulation of the muscle substance; perhaps in others the fibres get swollen up with fluid as the result of the sudden appearance inside them of a number of new molecules.[1] These, however, are guesses. Certain it is that a healthy man in training for the particular exercise performed, however severe that be, does not suffer from stiffness or soreness of any kind. Nurmi in a single afternoon is capable of breaking two world records, while in inter-university sports a competitor may often run well in two or even in three races, provided that sufficient intervals are given between them.

You will ask—I have often asked—what happens to the body in training? I am sorry, I do not know. Perhaps the blood supply to the active muscles becomes better, the capillaries responding more rapidly to the needs of the muscle; perhaps more

[1] The liberation of more molecules would cause a rise of "osmotic pressure" which would lead to a flow of fluid from the blood into the fibres and so cause them to swell up.

alkali is deposited in the fibres to neutralise the acid formed by exertion. More glycogen seems to be laid down in them as a store of energy, and certainly, among other things, they and the nervous system which governs them learn in training to work more economically. Perhaps by training the recovery process is quickened. Maybe the actual mechanical strength of the muscle-fibre and its surrounding membrane (sarcolemma) is increased by training, so that it can stand, without injury, the strains and stresses of violent effort. All these factors may be at work, but at present we can only point to the importance and interest of the problem, and suggest that someone should investigate it properly. The subject of acclimatisation to high altitudes, the means by which men who rapidly become mountain-sick at 15,000 feet, soon develop a tolerance to low oxygen pressures which will enable them in comfort to go much higher, have been widely studied in recent years. From the work which has been done on acclimatisation to high altitudes much has been learnt about the physiology of respiration. I am sure that if the same efforts were devoted to the study of training equally valuable results would be obtained. Perhaps the reason why people have investigated mountain-sickness and respiration at high altitudes so fully is that it gives them a good excuse for going off on an interesting and adventurous

journey. There is not quite the same inducement to study the physiology of training (though there is some, for it brings the observer to healthy places and into healthy company) but it does possess the advantage that it is much easier and less expensive to investigate. We know already so much about muscle that it seems a pity that in some directions we should know so little. The effects of training are very obvious and important, not only in games and sport, but in many sides of everyday life and work.

It is interesting to inquire how long recovery takes. It is easy to follow its course by means of measurements of the oxygen used in the process. Plates XIV to XVII show the apparatus used in measuring the oxygen consumption. In each case the subject carries a mouthpiece in his (or her) mouth and wears a nose-clip on the nose, so that breathing is only possible through the mouth. The mouthpiece is fitted with valves which allow fresh air from the outside to come in by one hole, No. 1, but prevent it from going out by the same hole again. The other valve allows the air expired to go out by a second hole, No. 2, but prevents it from being drawn back again into the lungs during inspiration. Thus, when air is drawn into the lungs it comes from the outside; when air is breathed out from the lungs it goes by opening No. 2, and travels down a

pipe to a tap which can be so turned that the air passes into a large india-rubber fabric bag, where it is collected. The air collected in the bag over a measured period is passed through a metre afterwards to determine its volume, and a sample of it is taken and analysed by an instrument known as a gas-analysis apparatus. Now the outside air which was breathed in is of known composition, or it can be measured in the same way, and the difference between the inspired and the expired air tells us how much oxygen has been used for each litre of air drawn in. If a man breathes in 100 litres of air in a minute, and if oxygen has been abstracted from the air in the lungs equal to 4 per cent. of its volume, then the consumption of oxygen per minute is 4 litres. We may measure the consumption of oxygen over a long period by making a prolonged collection of air in the bag, or we may divide the period up into short intervals, collecting the expired air in a set of smaller bags and measuring and analysing the contents of each separately. In the former case we measure directly the *whole* oxygen used in a given time; in the latter case we measure how much oxygen is used in each of the short intervals of which the longer interval is made up. Plate XIV, *a* shows a girl having her resting oxygen consumption measured in the laboratory. She is lying on a couch, and the bag into which she is breathing is seen

resting on her legs. She was found to be using about 200 c.c. ($\frac{1}{5}$ litre) of oxygen per minute. Plate XV, *b* shows similar apparatus being employed on a man walking. Plate XV, *a* shows a man swimming in a Swedish lake, with mouth-piece in his mouth connected by pipes to a bag carried in a boat which was rowed in front of him. As you see from such figures, the method is of very general utility; there is scarcely any form of exercise in which it cannot be used. In Plate XVII, *a* a similar experiment is shown on a man wheeling bricks, the object of the investigation being to find the load of bricks (and the speed of wheeling them) for which the cost of the work, as measured in oxygen consumption per brick carried, was as small as possible.

In following the process of recovery it is necessary to take a series of samples of the expired air in order to find the rate of oxygen consumption at various stages after the exercise ended. Fig. 38 is a diagram showing the rate of oxygen consumption before, during, and after exercise. The period of exercise is marked by a thick horizontal line. Directly exercise begins the rate of oxygen consumption starts to rise, as soon as it ceases it starts to fall. The exercise shown is of a moderate type, and recovery will be ended in a few minutes. After severe or exhausting exercise recovery may not be complete for an hour or more. The full rate of oxygen

consumption at the beginning of exercise is not attained for two to three minutes. It requires this time for the heart and lungs, and oxidation in the muscles, to work up to their full extent.

It remains now to analyse the interesting individual differences which must certainly exist between different individuals. Already there are indications that young and active persons recover more quickly than older and less active ones. It would

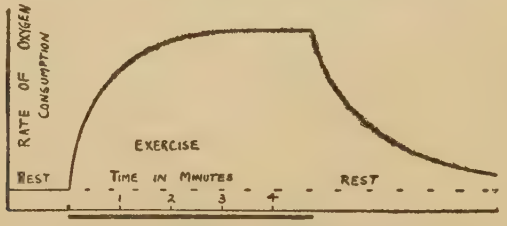


FIG. 38.—Rate of oxygen consumption before, during, and after exercise. The period of exercise is marked by a thick horizontal line.

be of the greatest interest to follow the recovery process in individuals differing widely in type and in muscular capacity in order to see whether, and how far, such differences do really exist, and on what they depend. If by understanding the factors at work in a faster recovery we were able to quicken recovery up, we should have done a great deal for the avoidance of human fatigue—unless people then started to work harder, which is what they would probably do!

There is a special importance in these experiments on the speed of the recovery process in connection

with "rest pauses." In heavy industrial work a man is naturally allowed to rest at intervals between his separate jobs. In athletic meetings different races are so spaced that a runner who wishes to compete in several events may have time to recover between them. In either case it is necessary to know the rate at which recovery proceeds, so that we may be able to decide how long a rest to give. In the case of a workman recovery need not be quite complete, since he is not exerting himself to his absolute limit in each effort, and the last stages of recovery take a very long time. The intervals therefore need not be long, since the earlier stages of recovery proceed rapidly. In the case of the athlete, if he is to do himself justice, for example, in the final heat of a 200-yards race, he must have recovered almost completely from his previous efforts before he starts, otherwise a certain amount of lactic acid remains free and unrestored in his body and muscles, and this causes a more rapid onset of fatigue when they begin to work again. The curves of fig. 39 show us the time required for various stages of recovery after fairly severe muscular work of short duration. In this figure full recovery is given as 100 per cent., and the various stages of recovery are given as percentages of full recovery. To say that a man is "80 per cent. recovered," means that of the total oxygen he is going to use in recovering he has

already used 80 per cent. Expressed in chemical terms, immediately at the end of the exercise there is a certain amount of lactic acid present in the muscles and body which has disappeared again completely by the end of recovery. At "80 per cent. recovery," 80 per cent. of this lactic acid has disappeared, only

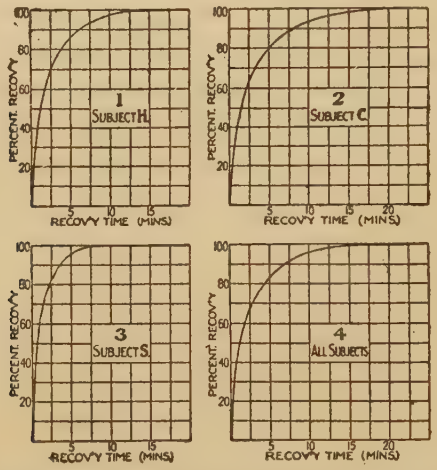


FIG. 39.—Curves of recovery for three different individuals and a mean curve, from fairly severe exercise of short duration. Vertically is shown the degree of recovery as per cent. of complete recovery; horizontally is shown time from the end of the exercise. (Sargent.)

20 per cent. of it remaining. It is obvious from the figure that the subjects H., C., and S. differ appreciably from one another. They are all healthy men: H. is a cross-country runner, aged 24; C. an ex-regular soldier, aged 35; S. an exceedingly powerful young man and an excellent swimmer. The exercise was vigorous "standing running," lasting for thirty seconds or one minute. It is obvious that S., who

would be picked out at once as the most powerful and athletic of the three, recovers more quickly than the other two. C., who although quite healthy, is older and does not have such opportunities for outdoor exercise as the others, is the slowest in his recovery. All these are normal healthy men, and there is no doubt that were we to make such experiments, on the one hand on the finest living athletes, and on the other hand on old people, on decrepit people, or on people suffering from disease, we should find enormously greater differences than those shown here. Differences therefore in the capacity of the body for muscular exercise depend, at any rate to some degree, upon differences in the rate at which recovery occurs; and remember that *during long-continued exercise recovery is taking place all the time*, and we can only keep up a given degree of exercise for a long time if recovery is able to keep pace with the breakdown processes that occur as a result of exertion.

Certain practical consequences can be deduced from the curves of fig. 39, but these must strictly be taken to refer only to exercise of the kind named, fairly (but not extremely) severe exercise for short intervals, such as half a minute or a minute. It is obvious that for such exercise in ordinary people recovery is complete within twenty minutes. Ninety per cent. of full recovery occurs, on the average, in

seven minutes; in subject S. it occurs in three and a half minutes. Thus, if we have to arrange a sports meeting with heats, semifinals, and finals, say of a 100-yards race, we are obviously allowing the runners time to recover between the different heats if we set these at intervals of twenty minutes or more. In industrial work, where in some trades severe efforts have to be made, it is obvious that two or three minutes of rest give the body time to recover to such a degree that it should be easy to start anew. In such work unduly prolonged rest-pauses are only a waste of time. The main part of the recovery is complete in two or three minutes, and since a workman is rarely going to the extreme limit of his capacity, it is not necessary for him to wait till he is absolutely recovered in order to start again.

Let me return now to describe how the work done by muscles, and the energy used by them, can be measured. In mechanics the word "work" has a perfectly definite meaning. If a force F acts upon a body, and we move the body against the force a distance x in a direction parallel to the force, the work done upon it is Fx. There are many ways in which this work can be measured in the case of the muscles of a man. For example, we may cause him to walk up a hill or a staircase and measure (1) the height through which he lifts himself, and (2)

the weight of his body. The product of his weight and the height gives us the work. If a man weighing 160 lbs. climbs a staircase 100 feet high, he has done work equal to 16,000 ft.-lbs.; if he does it in a minute he is exerting about half a horse-power, which is 33,000 ft.-lbs. a minute. It does not matter how steep the staircase or the hill may be, he does exactly the same work in lifting the body through the same height. In many cases of muscular effort the work done cannot so readily be measured. For example, in walking on the flat no external work in the stricter sense is done. An effort is made, energy is actually expended on the limbs in accelerating and retarding them, but all this is used up in friction inside the body itself, and apart from overcoming the small resistance exerted by the air no external work whatever is performed. It would require the most elaborate calculations to determine directly how much mechanical energy the muscles of the legs expend in such a relatively simple process as walking. The only practical way in which we can measure the energy spent by a man in such exercise is by a measurement of the oxygen he uses.

For laboratory experiments it is desirable to have some kind of machine on which work can be done without moving the body about from place to place. If we do not want to know exactly how great the work is, a simple form of exercise is "standing

running," a rapid jumping movement without progressing backwards or forwards (sometimes known to runners as "a hundred up"). In case, however, we wish to know the actual work performed, "standing running" is not suitable, as the energy is all wasted inside the body, is turned into heat, and never appears as external mechanical work. The simplest way, then, is to employ a bicycle ergometer, as shown in Plate XVI, *c*. In this instrument a bicycle frame is fixed on a wooden stand, and the back wheel is replaced by a heavy flywheel, round the rim of which, to act as a brake, passes a linen band which at each end is connected to a spring-balance. The instrument shown in the illustration is that designed by Dr. C. J. Martin, of the Lister Institute in London. Many other kinds of bicycle ergometers (work-measurers) have been made, but this is the simplest and least expensive, and works as well as any of them. The friction of the band on the flywheel can be adjusted by tightening it up, and the force with which the band resists the flywheel is measured on the spring-balances. If the edge of the wheel goes 100 feet against a friction of 5 lbs. weight measured on the balances, the work done is 500 ft.-lbs. and so can be accurately determined. The subject sits on the saddle and pedals round at a fixed rate given by a metronome or clock; the number of revolutions is read by a revolution counter,

such as one uses on the front wheel of a bicycle; knowing the circumference of the wheel and the number of revolutions, the total distance that its rim has travelled can be calculated, and this after multiplication by the force exerted on the spring-balance gives the amount of work performed. At the same time as the work is being recorded the air expired by the subject can be collected in a bag, and so the oxygen he uses can be measured.

There are other laboratory methods of measuring a man's work. Sometimes treadmills have been employed, in which the subject walks continually uphill inside a large wheel, which revolves at a fixed speed. In the same way a moving platform (Plate XVI, *b*) can be used (somewhat like a moving staircase in a Tube railway) on which the subject walks or runs at a rate determined by the speed of the platform. Such platforms are usually not very long, and when they are going fast, say at 12 miles an hour, it is very exciting work to run upon them. If the runner goes a little too slowly he is apt to be scraped off at the back: it certainly makes him keep up to have such a fear behind him. It is possible with this arrangement to have a blast of air blown upon the subject of the experiment, in order to keep him cool, while his friends can sit by his side as he runs and record what goes on in his body: and the instrument can be designed to tilt up or

down, so as to reproduce the conditions of walking, or running, up or down hill.

If we wish to compare the work done with the actual energy expended in the body we need to express both in the same units. One calorie of heat is defined as the energy required to warm 1 grm. of water 1° C. It is equal to the work done in raising a kilogram 42.4 cms., or expressed in an equation:

1 calorie = 0.424 kilogrammetre = 3.06 ft.-lbs.

Now the energy of our foodstuffs is known. It has been accurately measured in the laboratory. Usually we work in big Calories, distinguished by a capital C. A big Calorie is the heat required to warm 1 kg. of water 1° C.; it is equal to 424 kilogrammetres, or 3060 ft.-lbs. The energy required by a man in ordinary life has been accurately determined, and it is stated that the average man doing not too heavy work should receive in his diet about 3500 Calories per diem. Men doing heavy work require much more energy than this: 6000 to 8000 or even 10,000 Calories per diem is not an impossible amount for a man working really hard. Let us consider how this energy can be measured and how much food is necessary to supply it.

Food consists of three chief substances: proteins, fats, and carbohydrates. Of these, when oxidised in the body, proteins and carbohydrates liberate

about the same amount of energy, namely, about 4 Calories per grm. Fat is much more effective: when oxidised it yields about 9 Calories per grm. A pound of fat, when burnt, liberates enough energy, if employed with a 25 per cent. efficiency, to raise a 140 pound man 22,000 feet into the air. Thus, 3500 Calories would come from a diet consisting of 100 grms. ($3\frac{1}{2}$ ozs.) of protein, 100 grms. ($3\frac{1}{2}$ ozs.) of fat, and 550 grms. ($19\frac{1}{2}$ ozs.) of starch or sugar. The energy used by a man therefore may be calculated from his diet, provided that we know that he absorbs the whole of it. This method, however, applies only over long periods when we are sure that his body-weight has not changed, that he has not stored up some of the food, or that he has not, on the other hand, used food previously stored to supply himself with energy for work. If we wish accurately to find out how much energy a man uses during an ordinary interval of work, the only practical way is to measure how much oxygen he consumes. It is possible to put him directly into a large "calorimeter," an instrument for measuring heat directly. In such an instrument the heat produced, the oxygen used, and the carbonic acid set free can all be measured. The subject lies in a bed inside it, and may be supplied with a shelf, a telephone, a fan, and a light. By such experiments as these the "conservation of energy" has been established for the

case of men and animals, the energy given out as heat corresponding exactly to that liberated by the burning of foodstuffs. The method, however, is so laborious, involves so much apparatus, and cramps the subject's style so much, that for most purposes it is out of the question and we are left with the method of measuring his oxygen consumption.

The energy used is very simply calculated from the oxygen consumed. One litre of oxygen, when employed in the combustion of any of the ordinary foodstuffs, yields about 5 Calories of energy. Moreover, 1 litre of oxygen consumed means 1.34 grms. of sugar burnt (28.4 grms. = 1 oz.). Thus, knowing a man's oxygen consumption, we can calculate readily the amount of fuel (assumed to be sugar [1]) that he has oxidised and the amount of energy he has liberated. I will do so for a few interesting cases.

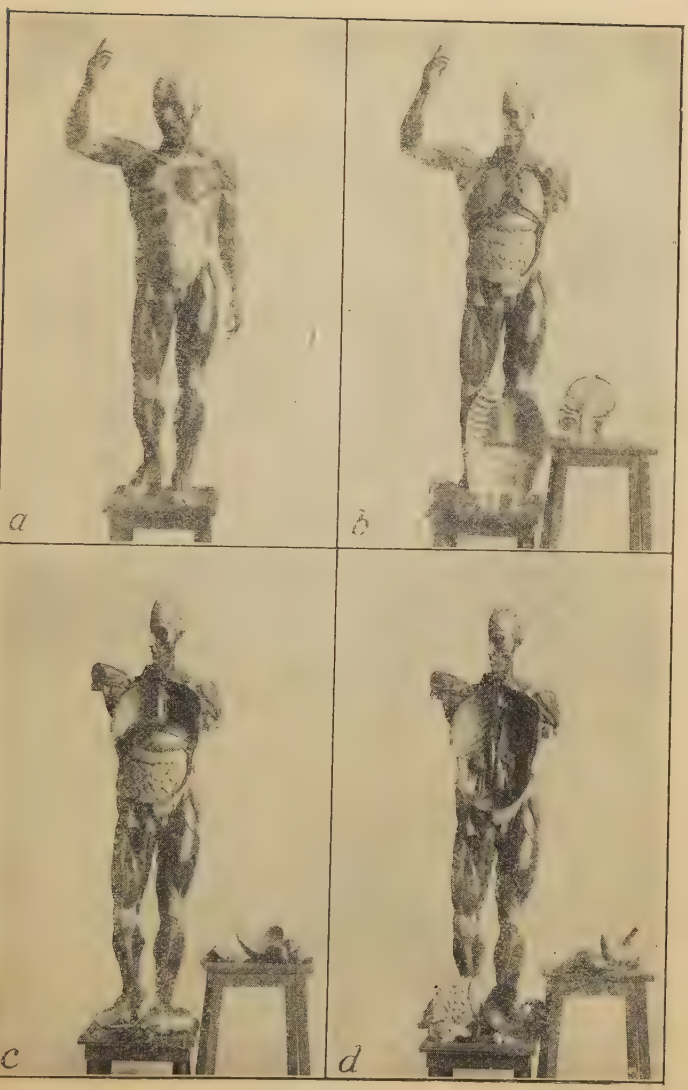
Let us consider first how much oxygen, energy, and food a man requires when he *remains completely at rest.* During rest there are all kinds of activities going on in his body—his heart is beating, his respiration is working, his muscles are in a state of tone, and various chemical processes are proceeding, all of which involve the liberation of heat. For these

[1] By measuring his respiratory quotient, *i.e.* the ratio of the CO_2 given out to the oxygen taken in, the nature of the food oxidised can be determined and so a slightly more accurate calculation can be made.

purposes in normal health he uses about a quarter of a litre of oxygen every minute, about 15 litres per hour, about 360 litres per day. Thus, at rest, he will be liberating heat to the extent of about 1800 Calories a day, half the amount required by a man doing ordinary, more or less sedentary, work. This would be enough, if he lost no heat, to raise his body temperature in a day about 25° C.; actually of course he is losing heat exactly as fast as he makes it, so that his body temperature remains constant. Even if he lost no heat whatever, it would take him an hour, while remaining at rest, to raise his temperature one degree. The method by which the resting oxygen consumption can be determined was shown in Plate XIV.

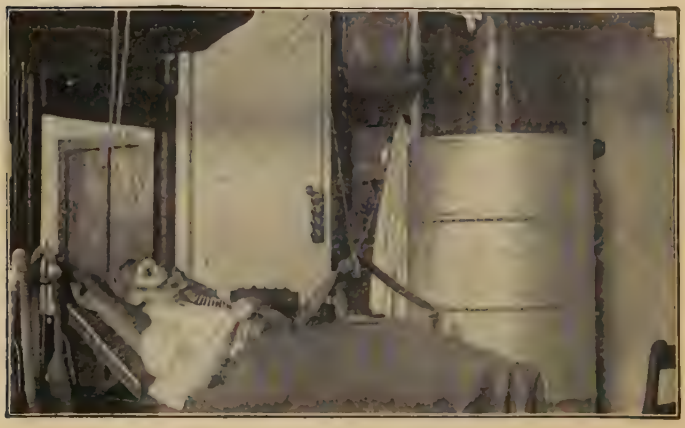
The oxygen consumption per minute of a man completely at rest, lying down, and fasting for some considerable time, say twelve hours before the experiment, is known as the "basal metabolism." This basal metabolism has been widely studied, both in physiology and in medicine. In ordinary people it is fairly constant and proportional to the total area of the body surface. In one interesting condition, however, it is greatly increased, namely, in the condition of "hyperthyroidism," as it is called, a state in which the activity of the thyroid gland in the neck is greatly enhanced. The behaviour and well-being of the body depend upon the proper

functioning of a number of glands which pour their secretions directly into the blood and so affect other parts of the body. The substances produced by the glands are to all intents and purposes drugs, usually singularly effective ones, working in almost incredibly small quantities, producing considerable effects, and having a large physical, mental, and even moral influence upon their owners. In recent years the discovery of these internal secretions has perhaps been overstressed, and a number of emotional people have rushed gaily to the conclusion that our behaviour, and even the history and evolution of the race, depend solely upon "glands." Most great discoveries are treated at first in this way, and the wildness of the suggestions which have been made must not detract our attention from the very real influence which these glands can exert. I have already mentioned one case, that of the suprarenals, which liberate adrenalin into the blood. The thyroid is another such gland, through producing a very different substance. If the thyroid does not function efficiently in a child he fails to grow properly, his bones remain short, he is stunted and idiotic, and is known as a cretin. In a grown-up person absence of the thyroid may lead to myxœdema, a slow pulse, a cold skin, a thickening and puffiness of the subcutaneous tissue, and a blunting of the mental faculties. If, on the contrary, the thyroid gland is



Models of a man. (*a*) Complete. (*b*) With half the head, one arm, and front of the body removed. (*c*) Heart and lungs removed. (*d*) Stomach, diaphragm, liver, spleen, and intestines removed (p. 129).

(*a*) Apparatus for measuring oxygen consumption of a subject at rest (pp. 140, 153).



(*b*) An alternative ("tank") method (pp. 140, 153).

overactive there is a rapid action of the heart, a flushed skin, wasting, general jumpiness, and inability to sit still and rest, sometimes a bulging of the eyes, and—the reason why I mentioned the thyroid in this connection—a large increase in the "basal metabolism" of the body. If the basal metabolism of a man be 30 to 50 per cent. higher than we should expect from his size, we may be fairly confident that he is suffering from an overactivity of his thyroid gland.

The function of the thyroid, and its gradual discovery and explanation are among the romances of science. For many years it had been known that removal, or absence, of the gland has untoward effects upon an animal or man but only recently has the active principle of the gland been isolated. This active principle is a substance known as "thyroxin." It has the unusual property, among materials found in the body, of containing the element iodine. It is an amazingly potent drug, and for years biochemists have been attempting to find out exactly what its chemical nature is and how it can be synthesised in the laboratory. That act in the drama of its discovery is now complete, as will be described in Lecture VII. Much more remains to be found out about the thyroid gland, and its activities, but another great step forward has been made in the conquest of living nature by biochemistry.

After this diversion we must return to our main theme. Before doing so, however, I must remark that in determining the amount of energy expended in doing any given job of work, we should remember that some of the oxygen used during its progress, and in recovery from it, is due, not to the work, but to this resting metabolism of the body, which it is impossible by any means to avoid. If we wish to know the oxygen consumption during work, we must measure the whole amount of oxygen consumed, and then subtract the amount which has been used in the resting processes alone. It is impossible to get rid of this resting liberation of energy. Everything else is superimposed upon or added to it. The oxygen consumption during work is determined, and the amount due to the work itself is obtained by subtracting the amount due to the resting processes.

Let us consider the case of walking, say, a mile. In my own case, standing still I use 0.35 litre of oxygen in a minute; walking at $3\frac{1}{2}$ miles an hour requires 1.06 litre per minute, so that the walking itself leads to an oxygen consumption of 0.71 litre per minute, a total for the mile of about 12 litres. The energy corresponding to this is about 60 Calories, enough to warm my body nearly 1° C. It takes some time to get warm walking at a moderate speed, even if little of the heat is lost. If the food

used to supply the energy be regarded as sugar, about 16 grms., rather more than half an ounce, of sugar will be used in the process. Walking at $3\frac{1}{2}$ miles an hour a healthy man in good condition should be able to go 30 miles in a day, or more if he has trained himself for the exercise. Reckoning his consumption again in terms of sugar or starch, a 30-mile walk should lead to the utilisation of just over 1 lb. of fuel. Actually, of course, in such a walk, part of the substance burnt will be fat, which has a higher energy value, so that on the whole rather less than a pound of foodstuffs, reckoned in the dry form, will be needed for such a 30-mile walk. Ordinary foodstuffs are largely water, which has no energy value. It is the dry weight of the food that matters.

Let us consider next what happens if we raise or lower the speed. Suppose that I walk a mile at the very low speed of 2 miles an hour. My oxygen consumption will be about 0.55 litre per minute, an excess of only 0.2 above my resting consumption. From this we calculate that only 6 litres (about a gallon and a third) will be required for walking 1 mile. The process is considerably more economical, the oxygen taken in and the fuel burnt being only about half as much as for the case of walking at an ordinary speed. Let us now take the opposite case, that of walking fast, at 5 miles an hour. Here my

oxygen consumption is 2.25 litres per minute, an amount 1.9 litres per minute in excess of the standing value. The oxygen consumed in walking a mile is now about 23 litres, the energy expended is about 115 Calories, enough to warm my body nearly 2° C. (that is why one gets hotter walking fast), and the amount of fuel burnt, reckoned as sugar, is about 31 grms., about 1.1 oz. To walk 15 miles in three hours (if I could do it) would require about 1 lb. of sugar to supply the necessary energy. You see from this how much more expensive it is in oxygen and energy to go fast than slow; by going fast we save time but we lose energy, and the speed at which we move is determined generally by balancing one of these factors against the other.

TABLE

Energy, Oxygen, and Food (reckoned as Sugar) used in Walking a Mile at Three Different Speeds

Miles per Hour.	Energy. Calories.	Rise of temperature, °C.	Oxygen used. Litres.	Food. Grms.	Food. Oz.
2	30	½	6	8	¼
3½	60	1	12	16	½
5	115	2	23	31	1

Note.—The rise of temperature is calculated on the assumption that no heat is lost during the walk. The result shows why walking fast in heavy clothes makes one hot.

In going very fast the heart, lungs and blood may be unable to keep up with the demand of the muscles for oxygen. Nevertheless, by measuring the oxygen used after the exercise, as well as during it, we can find how much oxygen has been used for any particular task. Let us take the case of running at top speed. A good "sprinter," running 120 yards as fast as he can go, uses during the exercise and in recovery from it about 7 litres of oxygen. Thus 12 litres, the amount needed for walking a mile at $3\frac{1}{2}$ miles an hour, would be sufficient only for 200 yards run at top speed; while 6 litres, the amount required to walk a mile in half an hour, would be sufficient only for 100 yards in ten seconds! This shows very clearly how wasteful high speeds are. On the other hand, running at comparatively low speeds is fairly economical. Thus running (or trotting, it can scarcely be called running at that speed) a mile in eight or nine minutes requires (on my part) only as much energy as walking it in twelve, which shows that if one is really in a great hurry to catch a train it is more economical (and it is certainly more comfortable) to run. A good runner, whom we have recently studied, requires only about 20 litres of oxygen to run a mile in six minutes, that is at 10 miles an hour. This is less than I should take to walk it in twelve minutes. A bad runner, whom we have studied too, would take 54 litres of oxygen to

run a mile in six minutes (if he could do it, which he cannot). You see, therefore, how much more economical some people are than others. One of the most important things in deciding whether a man can run (or do anything else) well is the economy with which he does it. If he uses a lot of energy he must get tired, if he uses only a little he will be able to last for a long time.

I have spoken a good deal about running because it is a subject which can very easily be studied, and the performance of a man in running can be readily measured. The differences between different people in respect of their power of running are very large, and in my last lecture we will consider them at greater length. The same methods, however, and the same calculations from them, apply to other forms of exertion. A swimmer may be connected by a pipe (Plate XV, *a*) to a bag carried in a boat in front of him, and so his oxygen consumption measured. Walking upstairs is an easy thing to study; walking up a moving staircase which is coming down, so that the subject would stay in the same place and the apparatus could be fixed by his side, would be still more easy. The energy expended in wheeling bricks has been measured (Plate XVII, *a*); it would be possible, though perhaps not very convenient, to measure the oxygen used by a coalminer working at a coal face. The

energy used in skating, ski-ing, climbing, bicycling, marching, even in pushing a motor-bicycle up a hill, has been determined. There is scarcely any form of muscular exercise or work which could not be studied in this way. In the last few years much has been learnt about bodily processes by such experiments. In the next few years more still will be learnt.

It need not be supposed that such experiments on the oxygen consumption are possible only in the case of man; animals, insects, or even fishes, can have their energy expenditure and their utilisation of oxygen measured in the same way, though often by very different methods. For example, the cockroach shown in a glass chamber in Plate XVII, *c* uses oxygen which can be measured by the apparatus shown in Plate XVII, *b*. He produces lactic acid if he be deprived of oxygen—he runs up an "oxygen debt" just as a man will do—he burns sugar and fat to supply himself with energy—he needs more energy if he takes more exercise. Some of the strangest creatures may be used to study a function, such as respiration, which is common to all life, and the result of studying such creatures is often to throw much light on the processes that occur in the human body. For some special reason—for example, a peculiarity of the creature studied—it may be much easier to solve some particular riddle, which has

been found very difficult in the case of man or the higher animals. The processes of life are fundamentally similar in all creatures—life did not start independently and in a thousand different ways, employing a thousand different processes, but probably from one main source, though the outward forms of the different creatures may be very varied and their inward arrangements correspondingly diverse. A fundamental process such as oxidation, energy liberation, the utilisation of food, is much the same in all living nature, although its details may appear to vary, so that we may often gain information of great value by studying the processes of life in the humblest creatures, such as that shown in Plate XVII, *c*.

LECTURE V

Nerves and Muscles Working Together

In my first lecture I spoke of the messages which come in along the nerve-fibres to tell us what is happening around or inside us. We will discuss now the little machines (or sense organs as they are called) which start these messages off. Some of them are obvious enough. At the back of the eye we have the most complete collection of them in the body. The eye is a camera, with a lens and a diaphragm in front of it: in place of the photographic plate at the back there is the retina, a layer of these little sensitive organs, each connected separately to a nerve-fibre running to the brain. When light falls upon one of them it starts sending messages along the fibre to which it is connected, and when a picture falls on the retina we get an impression made up of thousands of messages coming from all the sensitive end-organs and along all the nerve-fibres. These messages are pieced together by the brain to make up vision. Light is not the only thing, however, which can start these messages off. A simple experiment will convince you of this. If we bring a series of electric shocks into the head, for example,

by placing an electrode on the forehead, so that some of the current spreads into the retina, then each time a shock comes an effect is noticed—we *think* we see a flash (Plate XVIII, *a*). There is not really a flash—there is only a stimulation of the sensitive end-organs of the retina, which proceed to send messages along the nerve-fibres to the brain, which thereby gets the impression of light. You know the common expression "seeing stars" when you get a bang on the head or eyeball—that is the same thing, the retina is stimulated and sends messages to the brain, and the brain can do nothing but interpret these as light. Our senses can very easily be deceived.

Another obvious case of a sensitive end-organ is that of our ears. Behind the drum, which picks up the sound vibrations of the air, is a membrane which, according to Helmholtz, consists in effect of a series of little tuned receivers, each responding to some particular rate of oscillation. A pure note sets only one, or a few, of these in vibration: a complicated sound made up of all kinds of different notes—that is, of different frequencies of vibration of the air—sets a large number of these little tuned receivers oscillating, and so we get nerve messages coming from them to the brain, which interprets them as sound or speech. There is no difference in the messages themselves between these two cases of sight and hearing; the only distinction is that the

messages come in along different paths, and so we recognise them as different; the tradesmen come to the back door, the visitors to the front, but they are really the same kind of people.

There are other little "microphones," as we might call them, for picking up other kinds of messages. Inside our mouths and noses, dotted over the surface of the mucuous membrane, are many little receivers which give us the sense of smell and taste. Scattered over the skin (fig. 2) are other receivers, giving us the feelings of touch, heat, cold, or pain. Each feeling owns a special kind of receiver: the one which is sensitive to heat is not sensitive to touch or light: the one which gives us the idea of cold will not respond to pain or sound. Our ordinary sensations are made up of mixtures of these in various proportions. The taste of our food is made up of various different savours and smells; music is made up of different sounds.

Less obvious perhaps, but just as important to our well-being, are other sensitive receivers that I mentioned also in my first lecture, scattered about inside the body. In the muscles themselves are muscle-spindles (Plate XVIII, *b*) consisting of one or more muscle-fibres, enclosed in a sheath. One or more nerve-fibres pierce this sheath and make many spiral turns round the muscle-fibres, ending in a knob on the surface. When the muscle contracts,

messages are started off on these nerve-fibres and go towards the nervous system, giving us our "muscle sense." These muscle-spindles tell us what is happening in our muscles—whether they are contracting or being stretched and the force they are exerting. In the tendons of the muscles and in the joints are other receivers, telling us what is happening in them. Fig. 40 illustrates nerve-endings in the tendon of a muscle. The nerve-fibres branch

FIG. 40—Nerve-endings in the tendon of a muscle (Flack and Hill, after Hübner and de Witt).

and form "arborisations" (tree-like structures) on the surface of the tendon, and when the muscle pulls, the tendon is stretched and messages start off along the nerve-fibres and run to the nervous system. In connection with our ears, though nothing to do with the perception of sound, are other beautiful and sensitive mechanisms for telling us about our position in space, mentioning to us whether we are the right way up or not, informing us how fast we are turning and in what direction, concerned with the balance and what physiologists call the "posture" of the body. Plate XVIII, *c*, is a model

of the ear showing the three semi-circular canals which tell us about the rotation of the body. These canals (three to each ear), arranged in three planes at right angles to one another, are filled with lymph, and contain nerve-endings at one end. When the head is suddenly turned the lymph lags behind in one or other of these canals and presses on the corresponding nerve-endings, so telling us what is happening. If we continue to turn, the lymph soon takes up the motion of the head and ceases to press on the nerve-endings; but if we stop suddenly it continues its movement and gives us the impression that we are turning in the opposite direction.

How do we know how heavily an object is pressing on our skin? How loud a sound is? How bright a light? How heavy the weight we are holding in our hands? How cold an object we are touching? How hot the water in which we wash? Simple questions perhaps, but for many years they have been very difficult to answer. The difficulty lay here: that the messages which travel in a nerve are what are called "all or none"—either they travel or they do not travel, but if they travel they are independent of the strength of the stimulus that set them up. When a nerve sends off its message it is like a gun firing off its cartridge: if the cartridge explodes its force cannot be altered by pulling the trigger harder. If, then, the nerve can carry mes-

sages of only one size, how do we get stronger and weaker sensations from our end-organs?—as we undoubtedly do. The answer has just been given by Dr. Adrian at Cambridge, England.

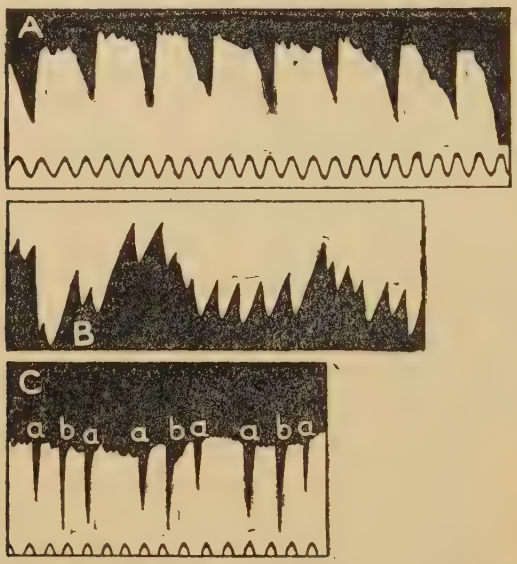


FIG. 41.—Records of response of sensory organs of sternocutaneous muscle of frog. The electric changes were enlarged by a 3-valve amplifier (×1850) (A) *one* organ: 35 responses per second due to hanging 3 grams on the muscle: (B) several organs responding together: (C) *two* organs, one giving a, a, a . . . , the other b, b, b . . . (Adrian and Zottermann).

In his experiments he employs a set of amplifying valves for magnifying the electric waves that run along a nerve-fibre when it carries a message. By a 2000-fold magnification these became much more easy to detect. So sensitive is the arrangement that the messages running along a *single* fibre in a nerve can be recorded on a photographic plate. A

little muscle of the frog—the sternocutaneous—was used, in which there are only a few sensitive end-organs capable of rseponding to a pull on the muscle. By cutting bits of the muscle away he could reduce it to the state in which it had only a single end-organ left. This little organ remained connected to its nerve-fibre, and the whole nerve containing the fibre was placed on silver wires, and the currents made when the muscle was stretched were led off. These were magnified by the amplifying valves and recorded in a dark room on a moving plate (fig. 41). When the muscle was pulled very gently the waves came along the nerve less frequently; when it was pulled harder more messages came. Each of these messages was the same—a stronger pull merely caused more of them to travel. The same experiment has been made in many ways and on many different parts of the body. Whenever anything is done which excites one of these sensitive end-organs, and so causes messages to run along its fibre (which would have caused "feeling" had the animal been alive), it is found that the greater the exciting cause, the greater is the frequency of the messages that come along as the result of it. The question therefore is answered. If anything feels hotter or heavier, or sounds louder or looks brighter, it is because it is *producing more messages every second* in the nerve-fibres that carry the sensation to the brain. A

stronger stimulus of course may sometimes send messages in more nerve-fibres than does a weaker stimulus, for example, by spreading out over a larger area and reaching more end-organs. But even if only the same number of fibres are set working it is possible to alter the "feeling" when the thing causing it is altered, simply by changing the number of messages which run every second along the sensory nerve-fibres to the nervous system. Our nervous systems are teeming with messages all the time, all finding their proper path, all graduated in intensity by means of the frequency with which they come, all causing the appropriate response.

What happens in answer to all these messages? Firstly, of course, they make us aware of what is happening to us and around us; they give our conscious selves the means of deciding whether to do anything, and if so what. They accomplish, however, much more than that. A message to the fire-brigade is more than a message—it is a command. We do not inform the fire-brigade that our house is alight merely because we think they will be interested. They start at once to come: an elaborate series of responses is set up by one message. So it is in the body. All this information that is coming in is not merely to interest you yourself that are sitting up aloft and admiring what is going on. Imperiously it calls up certain replies; it causes certain orders

(*a*) Apparatus for measuring oxygen consumption of a subject swimming (p. 141).

(*b*) Apparatus for measuring oxygen consumption of a subject walking (p. 141).

(*a*) Measurement of the "vital capacity" of the lungs. The pointer is set to zero. The subject takes in the deepest possible breath and then forces it all out—not too fast—through the meter. The largest reading of a series is generally taken as the correct value [illegible].

(*b*) A moving platform at the National Institute for Medical Research [illegible].

(*c*) Bicycle ergometer with a subject pedalling it round (p. 148).

to be sent to the muscles; even when we are apparently doing nothing, we are not really altogether at rest; our muscles are still showing a state of tone, they are not quite flaccid, they are supporting our limbs, maintaining our posture, keeping us in position, "standing by" like the fire-brigade ready for emergencies, and when accidents happen our muscles work immediately and quite automatically to put things right. If a fly settles on your face you brush it off; if you sit down upon a drawing-pin you get up again at once; if you slip or fall you try to save yourself, and often succeed long before you have had time to think about it. How is all this done? It occurs as an answer to the streams of messages that pour in and are sorted and arranged in the nervous system. If you are walking you do not consciously decide to take the next step, nor do you direct all the details of it. During the course of each movement, messages are coming in and telling you whether the movement is right, keeping you informed of the position occupied and the force exerted by your limbs and muscles; and in reply messages are going out again, to govern, perhaps slightly to alter, or adjust, the movements of your muscles, to keep them regulated or timed correctly.

The time occupied in a muscular movement may seem very short, but except in the case of a few very simple movements it is long enough for many things

to happen. When a man starts out to sail a boat from one place to another he does not just set his course once for all and fix his tiller; throughout the journey he is watching the wind and waves and tide, and making small adjustments to his sails and rudder. If a wave or a gust puts him out of his course he brings himself back again; there is a continual regulation of the boat to the conditions that exist outside it, or inside it. The rudder and the sails are not independent: if the setting of one is altered, the setting of the other must be altered too. Just the same process of play and interplay of the different parts of the body, reacting to each other and to the conditions outside, occurs in every movement of the muscles. In some diseases of the nervous system the "afferent neurones," as they are called, the lines which bring messages in, are affected, and the impulses which normally keep the nervous system informed of what is going on in the limbs and muscles no longer reach it. If the eyes are open movements can still be carried out and the posture maintained, but the movements are stilted, jerky, and unco-ordinated, while if the eyes be closed, the sufferer will sway violently and tend to fall. For skill, accuracy, and precision of movement, this continual play and interplay of messages, in and out, is essential.

These messages that go out in response to those

that come in differ from them in no way at all; they also are "all or none," they also travel at a high speed, they pass, however, along different lines, along "efferent" and not "afferent" neurones. They can be detected in the same manner, namely, by recording the electric changes which accompany their passage. Probably some hundreds of them reach the muscle-fibres every second. If a muscle be required to contract more strongly, messages come to it along *more* nerve-fibres and *more* muscle-fibres react. The only way in which the response of the muscle can be graduated is by means of adjusting the number of fibres in it that are stimulated. As regards sensation, the messages going in can be graduated by adjusting their frequency. With outcoming messages, however, no such graduation is possible; the muscle-fibre responds fully to forty or fifty impulses per second, and below that frequency it gives not a smooth contraction but one which shows a tremor. The only way in which we can exert a greater, or a smaller, force is by exciting a greater, or a smaller, number of fibres in the muscles that exert it.

All this interplay of ingoing messages and outgoing orders to the muscles is described as "reflex." The word implies the "reflection," the throwing back, of messages that reach the nervous system, Fig. 42 is a diagram of the simplest reflex. A mes-

sage comes in along the sensory nerve and excites a response in the motor nerve which causes a contraction of the appropriate muscle. Actually no reflex is quite so simple as this. The message has to pass through at least two or three "exchanges" before it starts out again; in complicated reflexes through a great number. These "exchanges" also send messages up to the higher parts of the nervous system

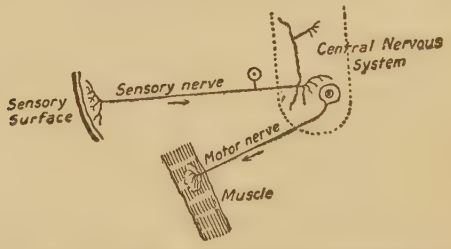


FIG. 42.—Diagram of the simplest reflex (Starling).

to keep the animal (or man) informed of what is happening; and they have their own activities modified by messages coming down from these higher parts.

There are many types of reflex, from the simple and rapid tendon jerk, of which the knee-jerk is the best known, to the most complicated set of movements which, by instinct or education, we learn to perform unconsciously. A man is placed in a sitting position, with one leg crossed over the other. When the tendon running from the patella (the knee-cap) to the tibia (the skin-bone) is tapped impulses are sent into the nervous system, where,

passing through the shortest possible system of exchanges, they are "reflected" back and the extensor muscles of the leg carry out a sudden and rapid kick. The time occupied is exceedingly short, only enough for the message to travel up to the spinal cord and back again and to excite the muscle, passing in the spinal cord only through a very few nerve-cells. It is entirely outside his control, he is aware of it only after it is complete. This is the simplest type of reflex; others, more complicated, are built up, involving more muscles, more limbs, until we get such things as the "scratch reflex" of the dog, or the secretion of saliva and the movements of the stomach of a hungry animal when he sees or smells food. Those of you who are expert bicycle riders will know how such reflexes can be educated. If you are an accomplished rider and skid on a slippery patch of road you often right yourself before you are aware of it. Only after you have saved yourself from falling do you realise that anything has happened (fig. 43). If you pick up a cat, and hold him feet upwards resting on the palms of your hands, and suddenly take your hands away, you will find that he will always drop on his feet (see Plate XXII). A high-speed kinematograph picture turned on more slowly ("slow motion") will show you how rapidly and how accurately his body has been turned round so that the feet are underneath. Even if

the cat is practically asleep in your hands, and even if you give him only a few inches to drop, you will find that he will succeed. He does not think it all out, he is probably unaware, until it is all over, that anything has happened; the whole business is automatic or reflex.

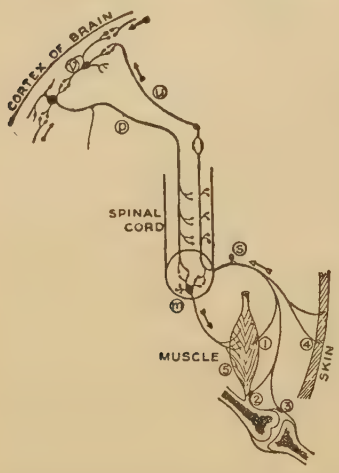


FIG. 43.—Diagram of the nervous system. (1, 2, 3 and 4) indicate the sensory nerve-fibres leading from muscle, tendon, joint, and skin, respectively, which are represented for simplicity as uniting into one sensory path before entering the spinal cord. The sensory messages from these fibres pass over to the motor neurones and cause an immediate reflex response in the muscle, and run up the spinal cord, passing into the cortex of the brain, where they are distributed and give conscious knowledge of the events happening in the body (Pear, *Skill in Work and Play*).

Those who have used a rifle or gun will know how difficult it is not to blink when it goes off: indeed, the inexpert are apt to blink *before* it goes off, so spoiling their aim. It is difficult not to start or jump when you hear a loud bang; it is impossible often to hide your emotions when something pleasant, or unpleasant, suddenly occurs. A very interesting example of this is the case of the so-called "psycho-galvanic reflex." The electrical "resistance" of a wire is what determines the current that passes when a given voltage is put across its ends. If a man puts his hands into two bowls of salt water with wires leading into them (as in Plate XII, *a*),

we can treat him as though he were a wire and measure his electrical resistance. When we have adjusted the "bridge" employed for the purpose, so that his resistance is recorded on it, a spot of light reflected from the mirror of a galvanometer stands still in the middle of a scale; if his resistance changes the spot of light shifts one way for an in-

FIG. 44.—Psycho-galvanic reflex. Deflection of a galvanometer produced by a change of electrical resistance in a human subject caused involuntarily by exciting his emotions (Einthoven).

crease, the other way for a decrease of resistance. Let us take a subject and connect him up with the Wheatstone's bridge, balancing the bridge so as to find his resistance, until the galvanometer rests in the middle of the scale. Let us keep him carefully quiet, without exciting his interest or emotions, and the spot stands still, perhaps with a slow and steady creep in one direction, which can be neutralised at intervals by readjusting the bridge. Now let us excite his emotions slightly: for example, by saying, what he may or may not believe, that we are going to prick him with a pin, or by suddenly clapping our hands, or by shining a sudden light in his face. Nothing happens for two or three seconds (see

fig. 44); then there is a sudden and large deflection of the galvanometer, travelling right over the scale and returning only slowly to its original position. The experiment is an extremely easy and effective one to make, and we find that the simplest threat (such, for example, as that we are going to cut his throat, which he certainly does not believe) produces a very large effect. We may read him out a list of names (preferably Christian names, of course of the opposite sex), and nothing much happens until some particular name is mentioned, which causes a vigorous response. We may draw what conclusions we like from the response, but one thing is certain, that the subject cannot prevent it; making up his mind that he will avoid any display of emotion, whatever happens, the galvanometer still reveals his secret. It is a beautiful experiment to make, and I recommend anyone who can borrow a resistance box, a two- or four-volt battery, and a galvanometer (even a sensitive pointer galvanometer will do) to make it on his friends. It is a "reflex"; it occurs in a hypnotised person just as in a normal one. It has a latent period of about three seconds; it involves a change of resistance which may be as great as 10 per cent. of the whole resistance between the two hands of the subject; it is entirely out of his control. It is one of those automatic mechanisms of which our being is made up.

The posture of the body, the position of it required for different purposes and functions, is maintained by the tonic contraction of the muscles. Not only must these assume a new tonic state in each new position of the body, but the tone of them must vary in harmony with voluntary and reflex contractions. Every voluntary act must be made with reference to the posture of the part involved. This tone is a weak contraction of the muscles, maintained reflexly by impulses coming from the end-organs in them and from the special organs of posture, the semi-circular canals and the otolith organ. Some muscles are "antagonist" to others: those that bend a limb are opposed by those that extend it; when one of them shortens the other gives way, its tone is abolished reflexly, to allow its antagonist to shorten. Just the opposite thing occurs to a muscle when it is suddenly extended by artificial means, instead of by the voluntary contraction of its antagonist. If an extensor muscle be suddenly pulled it responds by a brisk reflex contraction, evoked by messages to the nervous system from the sensory endings in it. Were it to do this whenever its antagonist contracted a state of rigidity would promptly result, one muscle pulling against the other. Nature has provided an automatic safeguard against this in a mechanism which is known as the "reciprocal inhibition of antagonist muscles." When an animal is

poisoned with strychnine this reciprocal arrangement is abolished, and in its place occurs a state in which, when one muscle contracts, its antagonist contracts too, causing the limb to go rigid. In tetanus infection, which leads to lockjaw, the sufferer is subjected to torture with every endeavour that he makes to open his jaw for the purpose of taking food or drink. The usual inhibition of the muscles that close the jaw does not occur, but instead they become excited and the jaw closes all the more firmly. Either poison acts inside the nervous system and reverses the usual arrangement by which one muscle relaxes whenever its antagonist proposes to contract. So automatic is this process in ordinary life that few people are aware of it at all; only by experiment is its existence realised, often by the experiment which Nature makes in disease.

The most complicated of the reflexes which an animal possesses are those which depend on education. They involve not only the spinal cord, but the cerebral hemispheres themselves. It is perhaps one of the greatest advances of modern physiology that Pavlov, the great Russian physiologist, and his colleagues should have succeeded in evolving methods by which, in lower animals, we can study the results of education and the powers of discrimination. All the methods employed by him depend on those reactions of the animal which are associated with

the taking of food. When food is placed in its mouth it excites a secretion of saliva—in common language, the animal's mouth waters: this is an "unconditioned reflex." Suppose, however, that every time food is given, a particular sound is made; after some time it will be found that the occurrence of the sound alone is sufficient to make the animal's mouth water: a "conditioned reflex" has been formed. Similarly sight or smell, or any other type of sensation, can be made to supply the stimulus for the conditioned reflex. In this way it is possible to measure the discrimination of a dog for sounds of different pitch, to ascertain how far one chain of reflexes interferes with another, how long it takes an animal to forget or to alter a reflex to which it has been educated. To quote only one result: an animal was trained to expect his food, and to respond by a watering of his mouth, when he heard a tuning-fork vibrating 100 times per second. It was found that no secretion of saliva was produced by a tuning-fork vibrating either 104 or 96 times, which shows an astonishing discrimination of pitch. In this way it is beginning to be possible to get inside the mind of an animal, and to learn something about the methods by which he can be educated and about the nature of his sensations. Perhaps the psycho-galvanic reflex might be similarly employed with chimpanzees, and so allow us to study the emotions,

and to follow the education of some of man's closest relations in the animal world.

The time occupied in a reflex action is greater the more complicated its nature; when only one possible response can take place it will be rapid. In the "knee-jerk" the time between striking the tendon and the beginning of the response in the extensor muscle is only about $5\frac{1}{2}$ thousandths of a second, of which only 2 thousandths are due to processes in the spinal cord itself. The "knee-jerk" is a very elementary reflex; in others, more elaborate, the time taken is much greater. It is easy to illustrate this by measuring a "reaction time." Let us arrange two electric keys and a lamp, so that when one key is pressed by the experimenter the lamp goes on, and as soon as the second key is pressed by the subject the light goes off again. The interval required by the subject to turn off the light can be measured by putting a galvanometer in parallel with the lamp, taking a certain fraction of the current; the deflection of the galvanometer will then record the time taken before the current is turned off (fig. 45). Such a "reaction time" will be short. Now let us introduce an element of discrimination. Let us have two lights, one on the right and one on the left, and a key for each of them. The subject does not know which light is going to be turned on, and it takes him longer to turn it off because he has to make up his mind

which to do. If we give him three lamps of different colours and three switches, one corresponding to each coloured lamp, the time taken will be still greater. The more complicated the reaction has to be, the longer it will take. In this experiment of course the reaction of the subject is largely a conscious one, and compared with the other parts of the nervous system, the brain itself, when it has to supply judgment or discrimination, is very slow. The same thing, however, applies in the case of reflexes, where the more complicated automatic movements take longer than the less complicated ones.

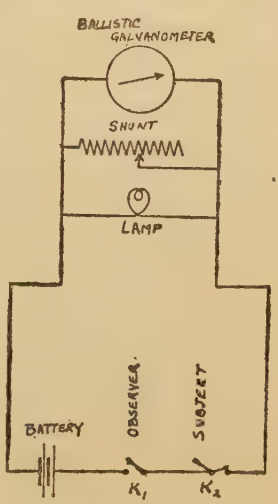


FIG. 45.—Arrangement to measure "reaction time." Note the battery and ballistic galvanometer with shunt. K_1 is the key closed by the operator; K_2 the key opened by the subject. The subject has to open K_2 as soon as possible after the light is turned on. The time taken in doing so is read from the deflection of the galvanometer on the scale.

It is interesting to ask how we learn to carry out these skilled and accurate movements, which we are always employing in work and play until they have become nearly, or entirely, automatic. When we remember how to make a movement, what is it we remember? Do we recall all the messages that we send out to the appropriate muscles—the timing of them, and

the adjustment of the strength of each response? The matter is one partly of psychology, partly of physiology, but there would seem to be some basis for the following answer. What we remember is not the messages we send out so much as the sensations we get. We remember a high jump, or the process of hammering a nail, or of writing our signature, largely by remembering the sensations which these give us.

Every movement, however simple, every posture, however common, produces whole groups of "feelings" through the network of sensory nerves which end in muscles, joints, and tendons, as well as in those more specialised organs of posture, the labyrinth or semi-circular canals, which tell us about the rotation of the body, and the otolith organs which tell us our direction in space (relative to gravity). In a posture we get what we may call a "standing picture" of what is happening to the body, supplied by the stream of messages that come in from all parts, including those which are in contact with the ground or with an external support. A posture in this sense, from the subjective stand-point, is a stationary set of sensations. With movement the picture is no longer stationary, but the time element is introduced. It is rather to be likened to a representation on a kinematograph. A jump, the throwing of a ball, the lifting of a cold and heavy metal shot,

the movements in a dance, are all remembered as a rapidly changing sequence of pictures made up of the sensations which every element of the movement provides. We do not remember how to make a movement by recalling what we look like in making it, though that is perhaps the way in which we remember it in others. To ourselves the movement is recalled by the sequence of sensations it provides. If we have a strongly developed "kinæsthetic" sense we may even interpret other people's movements in terms of the sensations which we picture ourselves receiving when we carry them out. There are no words in which to explain these sensations, but our capacity for skilled and accurate muscular efforts depends upon our memory of them, and upon our power of recalling them and evoking them again.[1]

[1] The matter has been discussed by Professor T. H. Pear in his book *Skill in Work and Play* (1924), and in a paper in the *British Journal of Psychology*, vol. xii, p. 163, 1921. In his book and paper Professor Pear emphasises that muscular skill possesses intellectual qualities which, although they cannot find expression in words, are nevertheless real enough things. The intelligent handling, analysis, and recalling of the sensations given us by movement, and our power of reproducing the movement in order to reproduce the sensations, are the means by which skilled movements are acquired. By experimenting with various types of movement, by noting which are successful, clean, and economical, which are clumsy and wasteful, and remembering the sensations accompanying either, we may learn to repeat and acquire

Accepting now the fact that all our movements are built up of reflex activities, welded and co-ordinated together as they become more complicated, by the governing power of the higher and conscious parts of the nervous system, we will turn next to consider a few feats of skill and concentrated power which we can accomplish by means of the machinery we possess. We know how complicated some of our movements are. The slow-motion kinematograph,[1] taking a large number of pictures (say 160) every second, which are then projected slowly on the screen (say at 16 a second), enables us to perceive and analyse these movements more accurately than is otherwise possible. It is very entertaining, and it is also very instructive, to see a woman dancing

those movements that are skilled and good. The physiological basis of all this is the complex network of afferent nerve-fibres which send messages from all the parts of the body concerned in movement. The psychological side is the sensations which all these messages evoke.

[1] It is possible to take far more than 160 kinematograph exposures per second in special cases. About 300 per second is the limit for a machine of the type in which the film is started and stopped for each exposure: but by electric-spark photography on a continuously moving film (the spark being practically instantaneous) it is possible to go to thousands of exposures per second, which, when put on the screen at 16 or so per second, allow us to witness the movements of the wings of an insect beating so slowly that we can analyse them in detail. Experiments of this kind are made at the Marey Institute in Paris.

or a man performing a high jump, or a dive, at one-tenth of the speed that we usually expect: some indeed of these films are wonderfully beautiful. The movements of the wings of a bird are too rapid in an ordinary way for us to perceive what motions are taking place: slow them down by the kinematograph and we can see at once the wonderful and well-adapted processes that occur in them. Having inspected and admired these processes by means of the slow-motion kinematograph, let us return to the real thing, and marvel at the skill of the nervous system in organising its affairs so rapidly.

If we take a good stop-watch, reading preferably to a fiftieth of a second, we can time an event which is not usually timed, the high jump; we can measure the interval between the moment when the feet leave the ground and that when they reach it again. When a man jumps 5 feet the time occupied is found to be about $\frac{4}{5}$ of a second. Half of this is occupied in going up, half in going down, and a very small fraction of a second in the middle is spent in wriggling the body over the bar. I say "wriggling." The time occupied in the jump allows us to calculate roughly how high the centre of gravity of the body has been raised: it is about $2\frac{1}{2}$ feet. Assuming that the original height of the centre of gravity of the jumper is about 3 feet, this means that in the high jump the centre of gravity goes about $5\frac{1}{2}$ feet high

into the air, which provides very little clearance when the height of the bar is 5 feet. Paradoxical as it may seem, it is possible for an object to pass over a bar while its centre of gravity passes beneath. A rope running over a pulley and falling on the other side is an obvious example. It is conceivable that by suitable contortions of the body the more accomplished high-jumpers may clear the bar without raising their centres of gravity above, or appreciably above, it. Others, less skilled, allow greater and greater clearance (see Plates XIX, XX, and XXI). In view of the great complexity and power of the movements, their rapidity, and the skill involved in them, it is striking that they can occur within a fraction of a second. In a high jump the mechanism of play and interplay of afferent and efferent nerves, and muscle-fibres, must be evoked in its highest degree.

Take again the case of throwing a cricket-ball. Even with the high gearing ratio with which they work, no human muscles are capable, in a simple movement, of producing a velocity comparable with that with which a cricket-ball is projected. Success in throwing, as in many other forms of rapid and violent movement, depends upon the employment of a *jerk*. Let us take the analogy of a whip in order to see what a jerk means. A long whip, tapering gradually to its tip, is swung round. By the mere

process of swinging no very great velocity is reached. At some stage, however, the whip is checked and a wave travels along the flexible tapering portion of it, concentrating the energy downwards into the thinner parts; finally, a considerable fraction of this energy reaches the end, the lightness of which ensures that for a given amount of energy an enormous velocity must be attained. The loud crack that a skilled performer can evoke with a whip implies that the tip of it is moving with a speed comparable with that of sound, and that a vacuum created behind it is being filled up. The crack is of the same nature as the "pop" that occurs when a vacuum flask, or an electric-light bulb, is broken, the air rushing in to fill the vacuum with a sudden and loud report. Thus, by the process of concentrating energy an enormous velocity can be attained at the end of the whip. The same thing happens when a skilled performer throws a cricket-ball. His body and limbs are rapidly moved, and at the appropriate moment a check is introduced which causes a jerk to pass along his arm, concentrating energy in his fingers, in which the ball is held. This is then projected with a velocity far greater than can be attained by a simple movement. To learn to throw well is a matter of long experience; many people indeed, especially women, never learn to do it. It is little wonder when we reflect on the extreme accuracy

with which every movement must be timed, those by which the momentum is created, those by which the check is introduced, those by which a jerk is propagated along a partly rigid body, the human arm. The world's record for throwing a cricket-ball is about 150 yards. Even neglecting the resistance of the air, which is probably an appreciable factor, this means a velocity of projection of 120 feet per second, about 80 miles per hour. A cricket-ball weighs about $5\frac{1}{4}$ ozs., from which the energy of its projection can be calculated. It is about 75 ft.-lbs., about 10 kilogrammetres. The work done in throwing a cricket-ball is not performed by the muscles of the arm, at any rate mainly, but is transmitted down the arm by a jerk produced by the sudden checking of the body and shoulders. If one further calculates that a considerable proportion of the arm itself is moving at a speed comparable with that of the cricket-ball, we get a far greater amount of work, a still more astonishing result.

Again we return to the question of the speed at which the process occurs. The hand is moving at 120 feet per second at the moment when the ball is projected with that velocity. Everything must be right, every adjustment made, the ball must be released precisely at the right moment, the jerk must be concentrated at exactly the correct place. The process is not thought out, it is realised and

remembered in one's muscular sense. The muscles and nerves are dealing with thousandths of a second. If the timing of one of the muscles were a few thousandths wrong, the throw would be a failure. A "record," so to speak, is turned on, as with an automatic piano-player; to that extent the movement is planned beforehand; but to secure the best result a continual adjustment is necessary, everything is being timed and regulated throughout by the play and interplay of nerves and muscles.

The accuracy with which we can do the same thing in precisely the same way, or in exactly the same time, is known to all of us. When I was a boy I used to amuse myself by seeing how accurately I could walk a mile in 1760 steps. My probable error in that distance was only about 10 yards. This was not due to sight, but to the muscular sense. A practised rifleman can bring his rifle to his shoulder with his eyes shut, so that when he opens them he will be looking along the sights. His nervous system can recall precisely, and repeat, the muscular sensations of the past. The precision of a painter or a draughtsman, the skill and grace of a dancer, even the accuracy with which all of us can write almost the identical signature every time, depend upon the same thing. Any good mile runner will tell you how he can hit off the time of the first lap of a mile race with an average error perhaps of not more than

half a second. The skilled gymnast, the automobile driver, and the aeroplane pilot all need this muscular sense in a high degree.

We all know about the dropping cat. The expression "falling upon one's feet" has become a commonplace in the language. A cat, asleep or awake, is taken in the hands and held feet upwards. To save it from a bump in case an accident happens (which it never seems to do) a cushion may be placed beneath. The hands are suddenly withdrawn and the cat falls (Plate XXII). There is no time to see what it does, but it lands upon the cushion on its feet. The slow-motion kinematograph enables us to analyse the movement, and we see how beautiful and well adjusted it is. It might have been thought to be a difficult problem, with no support in space, nothing from which to give itself a push off, for an animal to turn clean round in the air; a student of mechanics might even have been inclined at first to assert that it was impossible; the cat completes the process in a fifth of a second. It falls on its feet, it looks round, a little put about by what has happened, it walks away, somewhat annoyed, certainly not realising how clever it has been. If we are to speak with Professor Pear of the "intellectual respectability of muscular skill," we must admit that, in this respect, *Felis domestica* is much cleverer than *Homo sapiens*.

All this skilful movement, executed largely unconsciously by means of the beautiful mechanisms of ingoing and outgoing impulses, has an extraordinary importance in games and sports and in the processes of ordinary life. Not only can the skilful person do things which no one else can do, but even in simple tasks he can work more rapidly, with less effort and fatigue. In many things it is the last ounce that counts. It is often the things we can do when we are tired that matter. It is true in Kipling's words that, "If you can force your heart and nerves and sinew to serve your turn long after they are gone," then indeed you may inherit the earth. But success may be sought, not only in the "Will which says to them 'hold on,'" but in the skill required not to exhaust your patient machinery too early. If you can do with ease what others do laboriously, then when they are "finished" you will still be going on. Skill therefore is an essential part of endurance, and if you have endurance you will win.

LECTURE VI

Speed, Strength, and Endurance

It is common knowledge that some rates of movement are better than others. When we are on a bicycle there is one particular "gear ratio" which suits us best. If we ride up a hill a low gear is preferred; if we ride downhill, or with the wind behind us, a high gear. Again, in lifting heavy weights, or in carrying out difficult tasks, such as turning a stiff screw, we know that by slow and steady movements we can exert the greatest force. In carting earth from one place to another in a garden we require a spade and a wheelbarrow of a certain size. If these be too large, we exert ourselves unduly; if they be too small, we waste effort in moving them with too small a load. In running a race it is well known that it is not a good thing to go very fast at one time and very slow at others; there is a "best" speed. In climbing a mountain, going too fast leads to premature exhaustion; going too slow, on the other hand, is a waste of time, and does not prevent one from becoming fatigued. The question, therefore, of *speed of movement* is a very important one from the practical standpoint, and it is desirable to discover, if we can, the scientific basis of the facts

which workmen, athletes, sportsmen, and indeed all of us, have found out for ourselves, or learnt from others, concerning the best rates at which to work or move. In a previous lecture I spoke about the highest speed at which muscles can work, and I discussed the very great differences that exist in this respect between different muscles of the same animal and between those of different animals. We will consider now the same muscles working at various speeds.

In Plate XXIII, *a* is shown a machine consisting of a heavy flywheel mounted in ball-bearings on a stand. It is supplied with a number of pulleys of different size. A flexible wire can be wound round any one of these pulleys, and a subject can start up the flywheel by pulling on a handle attached to the end of the wire. Each pulley has a short peg standing out from it, round which goes a loop at the other end of the wire, so that it does not slip. When the wire is completely unwound the loop comes off the peg, and the wheel is free to rotate. The work done by the muscles of the upper arm in shortening, in the position shown in the figure, is communicated to the wheel, and can be measured by measuring the angular velocity of the wheel with a tachometer (speedometer). The whole of the work done by the muscles of the arm in shortening appears as the energy of motion (kinetic energy) of the wheel,

and this is ascertained by multiplying a constant depending upon the weight and dimensions of the wheel (the moment of inertia) by half the square of its angular velocity.[1]

The procedure is as follows: The subject takes the handle in his hand with his palm upwards; the loop on the wire is hooked over its peg on the pulley, and the wheel is wound up until the wire becomes tight. Then a pin is pushed into a hole in the side of the wheel so that it is held fast until the pin is withdrawn. The orders "get ready" followed by "go" are given, and the subject pulls as hard as he can on the handle. When his pull has been fully developed, which takes about half a second, the pin is suddenly withdrawn, his muscles shorten, the wheel spins round, and its speed is measured as soon as possible with the tachometer. A little simple arithmetic, or a table prepared beforehand, then gives the work done in foot-pounds or in kilogram-metres.

It is possible to vary the speed at which the muscles shorten. If the wire is wound round a very small pulley the arrangement will be like that of a very

[1] In the actual wheel shown the formula is

$$\text{Work in foot-pounds} = 6.5\left(\frac{x}{100}\right)^2,$$

where x is the speed produced in revolutions per minute. 400 r.p.m. is a very good effort. This corresponds to 104 ft.-lbs. of work done on the wheel.

high gear on a bicycle and the movement will occur only slowly. It may take several seconds to complete it. If, however, the wire is wound round a large pulley, it will be like a low gear, and the movements of the arm will occur very rapidly. Now the same muscular effort has been made in both cases. The subject has pulled as hard as he possibly can, and only when his full force has been developed is the wheel released. If we were to make the same

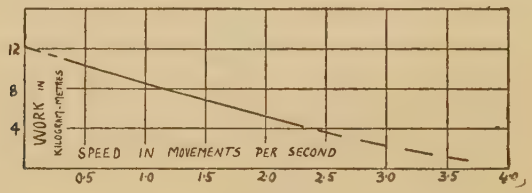


Fig. 46.

experiment with a steel spring instead of with a man's arm, stretching it always to the same extent by winding the wire up on one of the pulleys, we should always get the same work done on the wheel and the same final velocity, whatever the time occupied in shortening. With the human arm, however, the work done is very different in the two cases. When the shortening of the muscles is very slow a large amount of work is done; when the shortening is rapid, very little work. It is not exactly a case of "more haste less speed," but of "more speed less work."

Fig. 46 shows the relation between the greatest possible work done by the flexor muscles of the arm

in a single contraction, and the speed. The work is in kilogrammetres (1 kilogrammetre = $7\frac{1}{4}$ ft.-lbs.), and the speed is reckoned in movements per second. Actually only one movement is performed, and the speed is calculated by dividing unity by the time in seconds occupied by that movement. It is interesting to note (1) the enormous amount of work done by a pair of muscles which together weigh less than a pound, and (2) how this work is decreased by speed of movement.

The fact established by this experiment is quite general, and has considerable application and importance. As to the real cause of it I will only say that it is due to properties of the muscle which are intimately concerned with the nature of its mechanism, and which (under the title of the "viscous-elastic properties" of muscle) have had a good deal of research devoted to them within the last few years. I propose now only to consider some practical applications of the results.

Let us be clear as to what we have found. In a *single contraction* of the muscle the work done is greater if the external conditions be so arranged (for example, by giving it a greater load) that the work is done more slowly. More speed, less work in a single contraction; but please note—when you go on doing the same thing over and over again, you can do it more often in a given time if you move more

quickly, which *may* make up for the fact that you do less work in each movement.

An example of this is given in fig. 47. Suppose that 100 seconds are allowed and we want to see how much work a man can do in the time. We will assume that he always takes the same time, half a

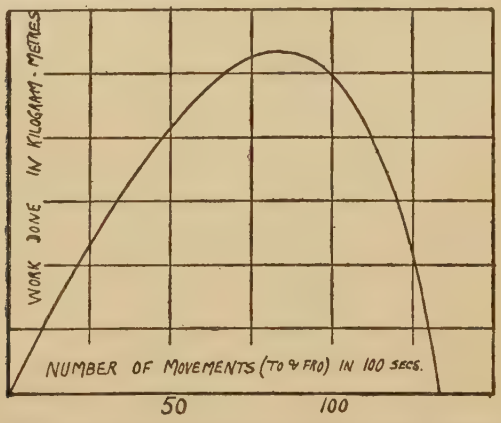


FIG. 47.—Work done in a given time (100 seconds) by the flexor muscles of the arm, as related to the number of separate movements by which the work is performed.

second, to relax his muscles and get in position for the next pull, and that the load is so adjusted every time that he can carry out any given number of pulls in the 100 seconds, from 133 on the high side to one on the low. In order to allow him to go as fast as 133 times in 100 seconds the load must be very small indeed, and the total work he can do will also be small. To prevent him from making more than one movement in 100 seconds the load must be enormous, and though he does a lot of work in

the one movement, the total amount of work again comes out small. From the curve we can see that at one particular speed, namely, about 85 movements in 100 seconds, the work is greatest. On either side of this speed it falls away, and for this particular process (allowing him half a second between strokes to relax his muscles) the best speed, the "optimum speed," as it is called, is 85 strokes per minute. At speeds higher than this it is a case again of "more speed less work," but on the lower side of the optimum the case is changed: here it is "less speed less work." Obviously, if we want to work at our best we have to choose the "optimum" speed, and skill in any kind of muscular movement consists largely in a choice of the speed at which it is performed.[1]

[1] In pulling against a machine of the kind shown in Plate XXIII, *a*, the work done follows fairly exactly the formula,

$$W = W_0\left(1 - \frac{k}{t}\right)$$

where W is the work done, W_0 and k are constants, and t is the time occupied in the contraction. In the case of an ordinary strong man, pulling as in Plate XXIII, *a* with his biceps and brachialis anticus muscles only, W_0 is about 10 kilogrammetres and k is about 0.25. If we allow half a second for relaxing the muscles between successive pulls, and imagine the man to work for 100 seconds, the work done in kilogrammetres will be

$$\left(\frac{1000}{t + 0{\cdot}25}\right)\left(1 - \frac{0{\cdot}25}{t}\right).$$

It is supposed that the muscles contract every time as hard as they can and show no fatigue. The curve of fig. 47 is calculated from this formula.

An obvious case, where a good deal depends upon the proper choice of the speed at which to work, is that of a bicycle. Most bicycles nowadays are supplied with three-speed gears. If you are going slowly up a hill, you employ a low gear so that your legs turn at about the same rate as when you are riding more rapidly on the flat. To pedal uphill on a high gear is tiring and wasteful, but no more so than to pedal on the flat on a low gear. Without worrying about the physiology of the matter, experience has led men to decide on the best gear ratio for various purposes. The short-distance racing bicyclist wants to do as much work as possible in a given time; the long-distance bicyclist, in whom economy is necessary, wants to do his work with the greatest sparing of energy. For each there is a "best" gear ratio, enabling him to work his legs at the "best" speed.

So far we have considered only the work done, but we often have to take account also of the energy expended in doing it; for a large amount of energy spent means fatigue, and fatigue causes us to stop or to cease doing our best. Now if a load is so great that the movement takes a very long time, the muscles have to be maintained in activity throughout the process, and this is wasteful in energy: to keep on pulling at an object, even if we cannot move it, and so do no work upon it, is tiring and expensive.

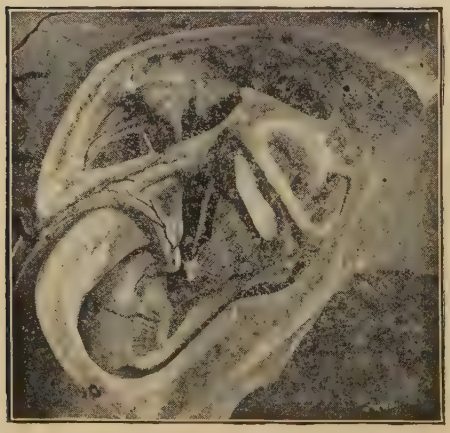
(*a*) Experiment on the oxygen consumption of a man wheeling bricks. By this means the "best" speed and the "best" load have been determined, *i.e.* those at which the energy used per brick is as small as possible (p. 141).

(*b*) Apparatus for measuring oxygen consumption of very small animals or insects, or of bits of surviving tissue (p. 161).

(*c*) A cockroach resting in a glass chamber while its oxygen consumption is being measured (p. 161).

(*a*) When an electric shock is brought into the forehead, some of the current will run through the retina at the back of the eye and stimulate the sensitive endings of the fibres of the optic nerve. These send messages to the brain which it interprets as "light" and the subject "sees" a flash (p. 164).

(*b*) A "muscle spindle" (p. 165).



(*c*) Model of the ear showing the three semicircular canals which tell us about the rotation of the body, (p. 166).

Thus if, on the one hand, we move our muscles too slowly by giving them a very heavy load the process is wasteful; we are spending energy in pulling, even though we are producing very little result. If, on the other hand, we move them too quickly it is also wasteful, but for a different reason, namely, that we do very little work in each movement. If we wish to be as economical as possible we must move

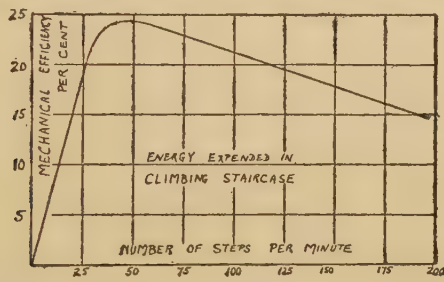


FIG. 48.—"Mechanical efficiency" of the process of climbing a staircase as related to the speed of climbing it. Speed in steps per minute; efficiency calculated (as a percentage) from the work done, and the energy required to do it, according to the relation,

$$\text{Mechanical efficiency} = 100\,\frac{\text{work done}}{\text{total energy used}}.$$

at a certain speed, or near to it. At other speeds the work is done inefficiently with an undue expenditure of energy. Fig. 48 shows an example of this in the case of a man climbing a staircase. The efficiency of working, or, in other words, the ratio of the work done to the energy expended in doing it, rises up to a certain speed and then falls off again. The height of the staircase in the experiment on which fig. 48 is based was about 40 feet, the number of vertical steps 78, and you can see from the figure that the

most efficient speed is one of about 48 steps a minute. The "best" or "most efficient" duration, therefore, of each step, is 1.3 second. If you try to go upstairs at this speed it will seem very slow, but in ordinary life we are not so much concerned with saving energy as with saving time. If we had to spend our whole day going upstairs, and wished to do the work as economically as possible, we should attain the greatest efficiency by going as slowly as shown in fig. 48. Here, again, there is a "best" speed, but the "best" is in respect of saving energy, and not, as in the case of fig. 47, of saving time.

The existence of these "optima" or "best conditions" is a very important thing, not only to those who are engaged in games, sports, and feats of endurance, but even more to those concerned with the processes of labour in industry. We want, on the one hand, to get as much as possible done in a given time, but, on the other hand, to get it done with the least expenditure of energy; for the using up of energy leads to fatigue, and continued fatigue to ill-health, inefficiency, and discontent. The subject of speed in relation to muscular work is one on which a whole book could be written. Here I wish to do no more than to call your attention to the existence of two different kinds of "best" speed, so that you may realise that such things exist, and when the time comes, or the need arises, find out more about them.

These "best" speeds do not always occur. For example, in running or walking on the flat the faster we go the more wasteful it is. As I showed in the last lecture, the slower you walk a mile the less energy you use. An "optimum" in respect of energy expenditure occurs only in such processes as involve the overcoming of some resistance outside the body. In walking or running on the flat there is no external resistance, only the movements of the limbs themselves, and there is no "optimum." Even here, however, if you wish to complete a given distance in a given time there *is* a best speed at which to go. To adopt it is very simple; you have merely to keep the speed absolutely the same throughout. You lose more energy by going fast sometimes than you gain by going slow at others. To run a mile in five minutes with the least fatigue you must keep up a speed of exactly 17.6 feet per second throughout. It has even been suggested (by Professor Kennelly of Boston) that the best way to break a running "record," *e.g.* in a mile race, would be to have wires round the track and a little signal flag dragged by a machine along the wire at a perfectly constant speed, so adjusted that the runner, if he kept up with it all the way, would just break the "record." This would prevent him from wasting energy by going too fast at some periods, too slow at others. Such artificial "pacing" would probably

lead to astonishing results if given a trial. In races against other people, as distinguished from attempts at record-breaking, the conditions are different: here it is often good tactics to induce your adversaries to do things, *e.g.* run too fast, or too slow, during some part of the race, which cause them more harm than yourself. A man who has a very powerful "finish" may try to persuade his competitors to go slowly during the race, so that he can keep up with them all the way, and then beat them in the "sprint" in. This is so much the case with cycling that the English 1-mile bicycling championship was won in 1897 in the extraordinary time of 5 minutes $52\frac{2}{5}$ seconds; it is easy to run it much faster than that: the 1-mile walking record is only about half a minute longer: which shows that winning races and breaking records may be very different things.

I have spoken so much about the most efficient speed, and about using the minimum of energy, because the power of doing things well, endurance, which means keeping up the same thing for a long time, and strength, which really means doing the greatest amount of work possible, all depend upon moving efficiently. If our muscles waste much energy we cannot keep up for long, nor can we do a large amount of work in a given time. Even that subtle thing called "skill" means, in the end, doing things as economically and with as little fuss as you can.

Skill, as we heard in the last lecture, depends upon the co-operation of muscles, nerves, and nervous system, but its end result is to do things with as little waste of energy as possible. If we waste little energy in doing a given job we shall be able to do it more often and with less fatigue.

It is possible in this way, in some cases at any rate, to give a quantitative measure of skill. No doubt there are forms of skill which cannot be expressed in this way. The skill of the mechanic, or the base-ball player, or the artist, does not depend simply upon the amount of energy he uses. In many things, however, skill is intimately concerned with energy, and by measuring the energy used in a given task we may measure inversely the skill with which it is performed. Let me take a simple case, that of running. Here we can easily measure the quantities involved, and when we succeed in measuring things we begin to understand them much better. Science consists first of observing things and of noticing their connections with one another, but science cannot advance very far until it begins to measure things too. Often we imagine that things are connected together, that *a* is the cause of *b*, but when we come to measure them quantitatively we may find that *b* is so much greater than *a* that it cannot possibly be due to it. On the other hand, we may find that *b* is exactly and quantitatively what

we should expect from *a*, which adds much to our idea that they are connected. We cannot always give a quantitative statement of muscular skill but the fact that we can measure it in running and in some allied cases, and give a numerical expression for it, is my excuse for reverting to running again.

In fig. 49 you will see four curves, or rather three, for two of them practically coincide with one another.

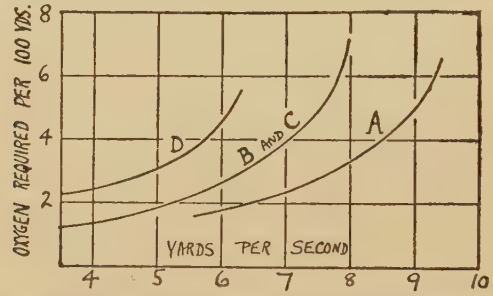


FIG. 49.—Energy used by four different runners over 100 yards at various speeds. Note (1) that the energy expenditure rises very rapidly as the speed increases, and (2) that the better the runner the less the energy expended at a given speed.

These curves correspond to four runners. One of them, A, is an experienced runner (a Cambridge "Blue"), and a fairly good performer at any distance from 100 yards to 2 miles. Two others, B and C, are moderately good runners, they are healthy, vigorous people, in good training; neither, however, as a runner is anything wonderful. The fourth one, D, is a very bad runner; he is an active, healthy person, he can swim five miles, he can stay in the English Channel for a quarter of an hour at the end of November, but he is not built for running; his

legs, perhaps, are too short, or his muscles too "viscous"; he says it is not his fault, but his parents'!

Fig. 49 shows the amount of energy used by these various people in running 100 yards at a series of different speeds. Horizontally is shown speed of running, vertically is shown the energy required to run 100 yards at that speed. The energy is expressed in terms of the oxygen required to supply the energy, but if you will, you can turn it into Calories by multiplying litres of oxygen by 5.14, or into ft.-lbs. by multiplying litres of oxygen by 15,860. You will see from the figure that at all speeds A is enormously more efficient than B and C, while D is very much less efficient. It is obvious, therefore, from these curves, which were obtained by laboratory measurements, that A will be able to keep up a given speed far longer than B or C, and enormously longer than D, because he spends so much less energy than any of them, because he is so much more skilled as a runner.

Now the reason why it is so important to run as economically as possible is that the amount of energy spent in running fast is so enormous. It does not matter that we should wind our watches with the least possible expenditure of energy; the amount is anyhow so small that even if it be multiplied 10 or 100 times it remains insignificant. In really violent effort, however, the amount of energy

expended is astonishing. Let us consider subject A, who has been far more carefully studied than the others. He weighs only 132 pounds, his vital capacity is 4.4 litres, the greatest average speed at which he ever went in an experiment was 9.2 yards per second—100 yards in $10\frac{4}{5}$ seconds. If it were possible for him (which of course it is not) to run continuously at this speed, he would require a total expenditure of energy equivalent to 13.7 horse-power. Naturally he cannot go on very long at such a speed; he rapidly expends all his available energy, lactic acid accumulates in his muscles, and he is forced to stop.

Let me put the matter in another way. If the whole of the energy required to allow him to run 100 yards in $10\frac{4}{5}$ seconds (and to recover from his effort) were used in lifting his body straight up into the air, he would travel vertically upwards 690 feet, two-thirds the height of the Eiffel Tower in Paris. The result seems ridiculous; in a sense it is, for we have assumed that the whole of the energy expended is turned into mechanical work: actually no machine has an efficiency of 100 per cent. Recent researches have shown that the actual propelling force exerted by a runner going at top speed is about 85% of his weight, so that in running 100 yds the mechanical work performed would be sufficient to raise his body 255 feet upwards. This calculation emphasises the extraordinary amount of energy

which is expended in really rapid and violent movements, and explains why it is that such efforts cannot be maintained for long.

People differ greatly from one another in strength: some are weak in some parts of their bodies, strong in others; some can keep up a force for a long time, while others get tired; some can put out an enormous amount of energy, others cannot. In the sense of being able to expend a vast amount of energy in a short time, the strength of a sprinter is great. He must use his energy efficiently if he is to be a good runner, but he cannot be a good runner unless in the last resort he possesses the capacity of expending energy very rapidly. A 12 horse-power motor-car may be very efficient, very well controlled, and altogether an admirable machine, but it will never win a race against another of the same weight which, reasonably well tuned up, can develop 50 horse-power instead of 12. So it is with men; a good short-distance runner must not only be efficient, but he must above everything be able to develop a high horse-power, be capable of expending energy rapidly. The reason why women cannot run so fast as men is simply that they cannot exert the same amount of force and energy.

There is one fundamental difference between the muscles of a man and the engine of a motorcar. If the car can do 1 mile at 100 miles an hour, it can

do 2, 5, 10, or even 50 miles at practically the same speed. Even very much greater distances than these do not appreciably "fatigue" it; it obtains all its energy by burning petrol actually at the moment it does the work. It does not need to "recover" after exertion. As soon as it stops the consumption of energy is finished—quite unlike the case of man. During a 100-yards run a man takes in practically no oxygen from outside, he works on energy that he has stored previously, and when the exercise is over he has to restore that energy by consuming oxygen and burning fuel. To put it in another way: by taking exercise he runs up an "oxygen debt," and when he stops he has to pay off that debt. The amount of oxygen taken in after the exercise is over, to allow the man to recover from the exercise, is called the "oxygen debt" at the end of exercise. Let me take an analogy to explain the matter more clearly.

If we wish to spend money we may do it, firstly, out of our income. This corresponds to exercise so moderate that it can be kept up for an indefinite time; the energy can be supplied by using oxygen taken in through the lungs during the exercise itself. Or, secondly, we can save up money beforehand for a long time and then spend it all rapidly when we need it. The body might work in this way, but it is better to express the matter otherwise. The third method

by which we may spend money is to borrow it, say from our bank, and then repay it afterwards. This is what we do in respect of oxygen. If the exercise is too severe to be paid for out of income, the body goes into debt and pays off the debt after the exercise is over. Now banks, if they are to lend one money, require security. The "security" on which the oxygen is borrowed for the body is the certainty that fatigue once incurred will be so strong a stimulus to the respiratory and circulatory systems that they will go on taking in oxygen and circulating it round in the blood until the debt is paid off. There are two different methods, therefore, of working: one, to live within our income and to depend simply upon oxygen which we take in during the exercise; the other, to depend on borrowing and on the oxygen which our muscles will have to take in after the exercise is over. These correspond to mild and severe exercise respectively. Various sorts of exercise come in between: when a man runs in a mile race he may take in about 16 litres while he is running (that is his income), and he may finish with an oxygen debt of 16 litres, corresponding to the energy he has borrowed. Short severe exercise depends entirely on borrowing; long-continued exercise almost entirely on income. The various stages between these two depend on both.

Now the endurance of a man is conditioned by

two things. In the matter of money the time he can go on spending at a given rate depends upon his income and upon the credit that his bank will allow. So it is in the body: the greater the income of oxygen during exercise, the longer a man can go on, and the more severe exercise he can undertake. The greater the oxygen debt which a man can incur, the more violently can he exert himself for a short interval, the longer will he be able to keep up an effort of given intensity. It is interesting therefore to inquire what are the actual values of these quantities—oxygen income and oxygen debt.

The greatest amount of oxygen that can be taken in by the lungs in a minute depends naturally on the size of the man, on the vital capacity of his lungs, on the rate at which his heart can force his blood around. The amount of work which the heart has to do is enormous, and it seems to reach its limit, in the case of athletic people, when about 4 litres of oxygen are taken in per minute. By breathing oxygen instead of air this amount can be increased, and the relief due to breathing oxygen during severe exertion is caused by the greater amount of oxygen which passes into the blood and so round to the muscles, heart, and brain, that need it. A man capable of absorbing 4 litres of oxygen a minute when breathing air can take in about 6 litres of oxygen a minute when breathing 50%

oxygen. Consequently if we were to set him to run in a hall or a tunnel filled with a rich oxygen mixture instead of air, his income would be increased by 50 per cent., and he would be able to spend energy at a correspondingly greater rate. The greatest oxygen debt he could incur would not be much increased thereby, so it would affect him little in the shorter distances. In the longer distances, however, there can be no question that a man running in such an atmosphere would break world "records" with ease. I should not be astonished if a mile champion, capable of running a mile in air in 4 minutes 15 seconds, who found himself in such an atmosphere, would be capable of doing it in less than 4 minutes. An important thing, moreover, is that, unlike the use of drugs, it would do him no harm. He could run faster in the oxygen than in the air, and he would finish only exactly as tired as if he had run in air, although having run considerably faster. It would be an interesting experiment to try, though rather expensive. If we suppose the tunnel to be circular, 8 feet high, 6 feet wide, and 200 yards round, it would contain about 30,000 cubic feet. If one-third of this were oxygen introduced from outside and the rest air, it would give us about the mixture we require. The total amount of oxygen introduced would then be 10,000 cubic feet; at half a cent a cubic foot it would cost about $500—rather

an expensive experiment, but still not an impossible one. It would cost far more to build the tunnel. Perhaps some sporting millionaire of scientific tastes would like to make it!

So much, then, for the question of oxygen income. Let us now consider the greatest size of the oxygen debt. This varies naturally with the type and size of man. In a powerful muscular man in good condition, weighing about 170 pounds, it is capable of reaching quite enormous values. Something between 15 and 20 litres of oxygen may be used in recovery from comparatively short periods of exertion—enough to keep a man going for more than an hour at rest. We may calculate from the magnitude of this oxygen debt the amount of lactic acid actually present in the muscles at the end of exercise. One litre of oxygen used in recovery implies the removal of 6 grms. of lactic acid from the muscles. Thus in the limit about 100 grms. (4 ozs.) of lactic acid may be liberated in the muscles of a man before complete exhaustion ensues. Lactic acid in the body is a strong acid. Its effect is about half as great as that of an equal weight of strong sulphuric acid; 100 grms. is nearly a quarter of a pound; you can imagine that serious results might follow the introduction of 2 ozs. of strong sulphuric acid into the muscles. They do occur with lactic acid, and we recognise them under the signs of fatigue and exhaustion.

How is it that a man can tolerate within his tissues such a large amount of acid? It is because he possesses in the fibres of his muscles a large reserve of alkali for neutralising this acid. As this becomes exhausted, the muscle becomes acid and is forced to stop. It is probable that this capacity of the muscle for neutralising acid formed inside it, and for tolerating its presence there, not ceasing

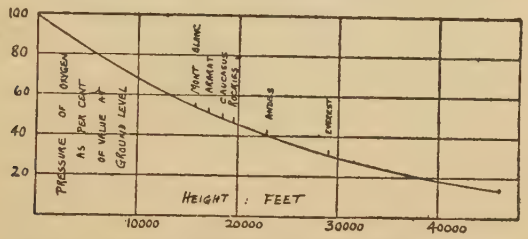


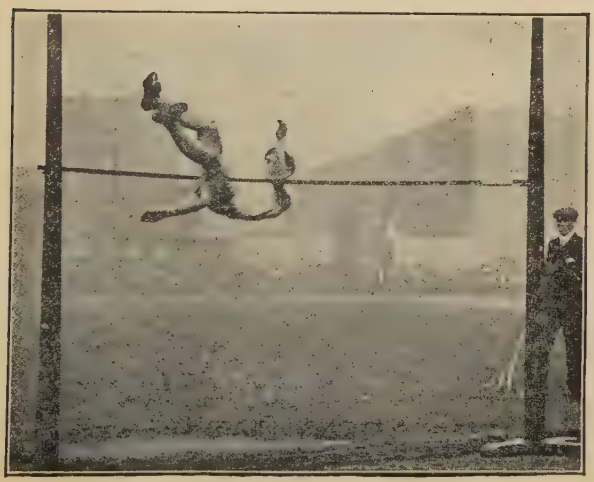
FIG. 50.—Pressure of oxygen (or air) at various heights as a percentage of the value on the ground. Pressure of oxygen at sea-level is about 0.21 of an atmosphere: at 18,700 ft. it is 0.10 of an atmosphere.

to go on directly the acid content rises, is one of the factors that distinguish an athlete from an ordinary person. The degree of effort we can tolerate is largely a matter of the amount of acid we can stand. This may seem a prosaic way of describing athletic achievements, but not so prosaic as the undoubted fact that all human intelligence depends upon the proper functioning of the thyroid gland, and ceases in a few seconds if breathing stops.

There are many forms of sport and adventure where success depends upon the capacity of the body for undertaking violent efforts when required,

or for enduring and overcoming fatigue. Let us take the case of mountain-climbing. The effort of climbing is in itself severe, but its severity is greatly enhanced by the low pressure of oxygen that exists at high altitudes. The pressure of oxygen at 18,000 feet is only half of what it is at sea-level. At 27,000 feet it is about one-third (fig. 50). Now you have heard already how an increase in the pressure of oxygen in the air breathed can make a man go faster, will allow him to take more oxygen per minute into his blood and muscles; the opposite effect is produced by a fall in the oxygen pressure, and it is well known to all who have climbed high in mountains that sickness comes on, caused by lack of oxygen, at a height somewhere between 10,000 and 14,000 feet. If a man remains at this height he fairly rapidly becomes "acclimatised"; more blood corpuscles appear in his blood to carry oxygen, the ventilation of his lungs is increased, and his body learns to tolerate the absence of oxygen. He is still unable to take as severe exercise as at sea-level, and his face may show a permanent bluish colour betokening the incomplete saturation of his blood with oxygen. He may, however, remain there for years and be healthy and comfortable. If he goes still higher the symptoms appear again, and again he may become acclimatised. In spite, however, of the acclimatisation, as he proceeds higher

(*a*)



(*b*)

(*a*) and (*b*) A skilled high-jumper (A. C. Bellerby, Cambridge University) just clearing the bar (pp. 187, 188).

(a)

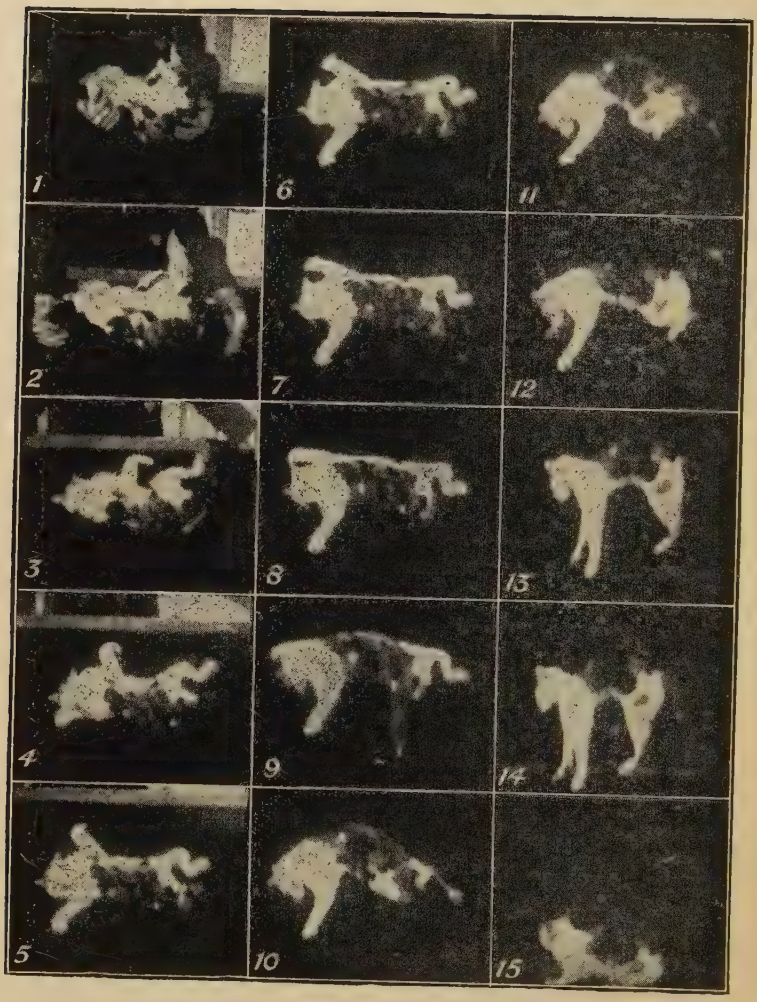
(b)

(*a*) and (*b*) Less skilled high-jumpers (aged 11 and 10) clearing the bar (*cf.* Plate XIX), (p. 188).

(*a*)

(*b*)

(*a*) and (*b*) Still less skilled high-jumpers (aged 7 and 6), allowing still greater clearance (*cf.* Plates XIX and XX), (p. 188).



The dropping cat: about 160 exposures per second. The cat is held feet upward and the hands are suddenly withdrawn. Note how quickly the animal has turned over. 1–15 are at intervals from the start of 0, ·05, ·10, ·125, ·141, ·149, ·157, ·165, ·181, ·236, ·33, ·43, ·465, ·48, ·50 second (p. 192).

he becomes less and less capable of severe muscular effort. For this he needs a good oxygen supply, and since the pressure of the air is so low he is unable to get it. The only method of relief is one adopted by flying men, namely, to carry a supply of pure oxygen, which is mixed with the air and so raises the oxygen pressure. That is easily accomplished in an aeroplane, but in the case of a mountain-climber it is difficult, or impossible, to carry oxygen for more than occasional use. The climbing of Mount Everest is largely a problem of overcoming the prosaic physiological difficulties associated with a low pressure of oxygen, and the only people who are likely to succeed are those whose lungs, hearts, and circulations are able naturally to supply them with oxygen in large quantities. It is impossible to trust to oxygen in cylinders: among other things these weigh too much. If a champion Marathon runner were also a skilled climber he would be as likely as anyone to reach and return from the top of Everest.

At high altitudes the oxygen income is necessarily so small, owing to the lowness of the oxygen pressure, that almost all effort except the very gentlest has to be made by the process of running into debt, this debt being paid off in recovery afterwards. It is necessary, if a violent effort is to be undertaken, to make it quickly, and then stop for a long period

to recover. At great heights there is no question of plodding on, you must make your effort and then stand still to recover. If your income is very small, you can only spend by borrowing.

Success in games and sports depends upon other things, of course, as well as power and skill in expending energy. There are some who feel that the scientific study of sport and athletics will take all the romance out of them—it is almost as bad as neglecting to take off your hat on going into church! No doubt there were those, probably there still are, who say, or feel, that the heavens would be much more beautiful if the astronomers had not attempted to find out their secrets. There are even people who object, on principle, to insulin or diphtheria antitoxin! To such people one can only retort that they are welcome to remain in ignorance if they please, but they must kindly let the rest of us go on finding out about things if we want to. I admit that in the "make up" of a champion athlete there is much more than the mere mechanism of his muscles and body. I know perfectly well that moral qualities of courage, restraint, and resolution, mental qualities of skill and understanding, go to the making of a good performer in whatever pursuit, of work or play. The fact remains, however, that the chief factor in many forms of athletic achievement is the supply of energy and its proper and economical

utilisation. I will finish with an example which I hope will convince you, the case of the runner A, whose curve is shown in fig. 49, and an experiment on whom is shown in Plate XXIII, *b*.

This runner has, so far as we have been able to find, a maximum oxygen debt of about 13.7 litres. His greatest oxygen intake is such that in one minute, starting from rest, he can take in 1.7 litres, in two minutes 4.9 litres, in four minutes 11.8 litres, in ten minutes 32.7 litres. Now we may suppose that he finishes a race completely exhausted; if not, he ought to have gone faster: he has used the whole of the oxygen of his income and he has exhausted all the credit which his bank will allow. In one minute, therefore, he has taken in 1.7 litres and he has borrowed 13.7, a total of 15.4. He has 15.4 litres of oxygen to spend in a minute; we can look up on a curve similar to that of fig. 49, but expressing oxygen requirement per minute (and not per 100 yards) as a function of speed, the velocity to which this corresponds. We find it is about 480 yards per minute. In the two-minute run he has 13.7 to borrow as before, and 4.9 out of income, a total of 18.6; 9.3 per minute, which from the curve corresponds to about 440 yards per minute. In the case of the four-minute run, again he can borrow 13.7, and he can take in 11.8, a total of 25.5, which is 6.4 per minute. Again we look up on the

curve and we find a speed of 387 yards per minute. In the case of the ten-minute run, once again 13.7 litres borrowed, 32.7 litres income, 46.4 altogether—4.64 litres per minute, 348 yards per minute. These are the highest speeds which we could expect our subject to attain if he were completely to exhaust himself in the times named. Now he happens to know his best times at a series of distances, and these can be compared with those obtained by calculation as above. The following table, taken from a paper by Sargent (*Proc. Roy. Soc.*, B, vol. 100, p. 11, 1926) shows the degree of agreement obtained. It is good—almost too good to be true; in another experiment the agreement would probably not be so exact.

TABLE

Distance.	300 yds.	$\frac{1}{4}$ mile.	$\frac{1}{3}$ mile.	$\frac{1}{2}$ mile.	1 mile.	2 miles.
Calculated best time.	33.3 s.	51.5 s.	1 m. 12$\frac{1}{2}$ s.	2 m. 1 s.	4 m. 41 s.	10 m. 12 s.
A's actual best time.	34 s.	51.4 s.	1 m. 15 s.	2 m. 2 s.	4 m. 40 s.	10 m. 10 s.

The table shows, however (and it is based upon many experiments), that the performance of a subject can be deduced fairly accurately from considerations of energy and oxygen consumption alone. We have to make him run and to measure the efficiency with which he does it, and record it on a curve similar to that of fig. 49. We must measure his

greatest possible income of oxygen, his greatest possible oxygen debt, and then we have all the data for calculating the greatest speed at which he can run any required distance. I am confident that if this process be repeated with sufficient care on other athletes we shall find in general the same thing. Indeed, since it is exhaustion, oxygen want, lactic acid, which stop him, it is practically certain that such considerations will hold. Thus, in a way, we have succeeded by laboratory tests in measuring and establishing the chief factors in athletic prowess.

So much, then, for the mechanism of nerves and muscles. This is an age of engineering, an age when all people employ, many people can make, and some people even can understand, machinery. We all must use, every moment of our lives, the machinery which Nature has provided in our bodies, and many of us enjoy the use of it and delight to work it well. We cannot learn to make it, for it makes itself as we grow, though we can help it or injure it in the making. We can, however, try to understand it, and many of you I know will agree that there is much more pleasure in using a machine which you can understand. There are few small boys, and not many grown men, who do not want to take machinery apart to see how it works. We cannot do this with our bodies, but there are other ways of finding out about them. We cannot hope yet to understand our

living mechanisms fully, but even the little we know already can add delight to physical exertion, and can make us realise the complexity of muscular skill, the nature of strength and endurance; and the effort to understand will help us to appreciate the beauty and wonder of the devices with which our bodies are endowed.

LECTURE VI

Appendix I

The world's records for various kinds of racing, which can be found in books of reference such as *Whitaker's Almanac*, or the *World Almanac and Book of Facts*, provide a very interesting study if they are treated graphically. In a presidential address to the Physiology Section of the British Association at Southampton in 1925, I discussed the physiological basis of athletic records, and in the printed paper will be found various diagrams relating the average speed of an event to the total time occupied in it. Curves are given there for men running, women running, men swimming, women swimming, men rowing a boat, men bicycling, horses running, and men skating. Some of these curves are given in fig. 51. In a general way the form of these curves can be explained by means of such considerations as are given in the above lecture. One interesting thing can be noticed from the curves, namely, that some of the records lie *below* the line passing through the other ones, while others lie slightly above it. Those points that lie below the curve are records which it will be relatively easy to beat, those above the curve will be very difficult. The latter probably represent the events to which most attention has been devoted by athletes, such distances as $\frac{1}{4}$ mile and 1 mile.

The same kind of curve is always found in all kinds of racing. As we pass from the shorter to the greater distances, the average speed at first increases a little; this is due to the starting inertia of the body, a purely mechanical factor. There is a total time lag in starting up, due to inertia, of about 1 second. This naturally has a greater relative effect in a short race than in a long one, and the 220 yards is run at an appreciably higher average

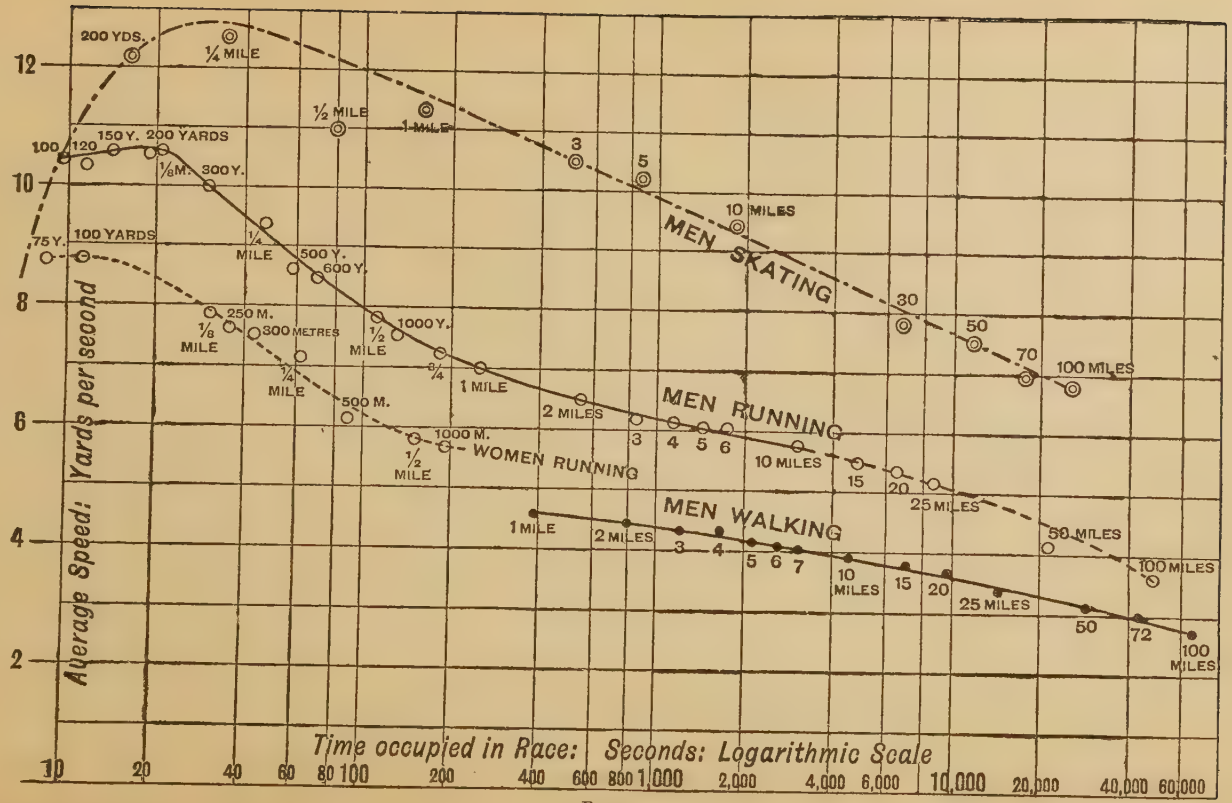

Average Speed: Yards per second
Time occupied in Race: Seconds: Logarithmic Scale
MEN SKATING
MEN RUNNING
WOMEN RUNNING
MEN WALKING
200 YDS.
¼ MILE
½ MILE
1 MILE
100
120
150 Y.
200 YARDS
⅛M.
300 Y.
75 Y.
100 YARDS
¼ MILE
500 Y.
600 Y.
250 M.
⅛ MILE
300 METRES
¼ MILE
500 M.
1000 Y.
½ MILE
¾
1 MILE
2 MILES
3
4
5
6
10 MILES
15
20
25 MILES
30
50
70
100 MILES
1000 M.
½ MILE
1 MILE
2 MILES
3
4
5
6
7
10 MILES
15
20
25 MILES
50
72
100 MILES
12
10
8
6
4
2
10
20
40
60
80
100
200
400
600
800
1,000
2,000
4,000
6,000
10,000
20,000
40,000
60,000

FIG. 51.

speed than the 100 yards. Already, however, there is a considerable falling off in real speed. Taking the 100 yds. record as $9\frac{3}{5}$ secs., and allowing 1 sec. lag, the speed in 100 yds. is 11.6 yds. per sec.: taking the 220 yds. record as $20\frac{4}{5}$ secs. and allowing 10 secs. for the first 100 yards we have $10\frac{4}{5}$ secs. for the last 120 yards, 11.1 yards per sec. over that part of the race: noticeably less than 11.6. At $\frac{1}{2}$ mile the average velocity is only about three-quarters of what it is in 220 yards, though it is 25 miles before it has come down to a half. You can see easily from the curves how extremely fatiguing the most rapid movement must be, how short a time it can be kept up. This is just what has been found in the experiments described in Lecture VI. At half the maximum speed the effort can be kept up for hours instead of only for seconds.

It is astonishing how many people have studied the results of athletics and racing, by plotting them graphically and attempting to find equations to the curves obtained. Since I began to work on the physiology of the subject a number of these have written, sending published papers of their results. Of these perhaps the most notable is that of Professor Kennelly, of Boston (*Proc. American Acad. of Arts and Sciences*, vol. 42, p. 275, 1906; vol. 61, p. 487, 1926). By plotting the logarithm of the distance covered (or of the average speed) against the logarithm of the time occupied he gets curves which are approximately straight lines over a wide range. Fig. 52 shows the present world's running records plotted in this way. It is doubtful, however, how far the simple relation described by Kennelly really represents the physiological facts, and the line is obviously not quite straight. From the standpoint of physiology the chief factor in determining the speed at which a run of given distance can be performed is the amount of energy expended, and the equations derived from this assumption would be quite different from those employed by Kennelly. Moreover, there are actually other complicating factors which make it unlikely that any simple equation will apply exactly.

From the point of view of the scientific study of athletics, these graphical representations of the world's records are complicated by the fact that they are made on a variety of different individuals. The man who can run 100 yards well is not the same man as, nor is he usually even similar in type and build to, the man who can run 10 miles well—indeed, in many cases

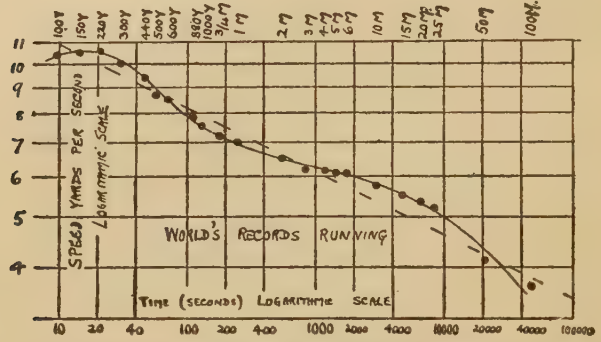


FIG. 52.—Present-day world's running records plotted: the logarithm of the average speed in yards per second is given vertically, that of the time taken horizontally. The resulting relation is approximately linear as shown by the broken line. More strictly it is a curve as shown by the full line drawn through the points. Each point represents a world's record, the distance being noted along the top in yards (Y) or miles (M).

he is very different. Inside, in their internal mechanisms, the two are even more diverse. The long-distance runner must be economical in his movements, the short-distance runner requires chiefly an enormous maximum horse-power. In order to get results capable of being analysed completely on a physiological basis we ought to obtain them on a single individual. We should require a performer trained and skilled in the particular type of exercise being studied (walking, running, swimming, etc.), and the same man, kept in a constant state of training, would have to ascertain his best times for a series of distances from the shortest to the longest. This would avoid the complicating factor of having the various distances done by different people. Actually the experiment described

in Lecture VI on the subject A is the beginning of such an attempt to study athletics quantitatively. It is hoped in the future to carry out more extensive experiments on the same lines.

LECTURE VI

Appendix II

In the scientific study of athletics one thing particularly is needed, namely, accurate timing of the runners, not only over the whole race, but through individual stretches of it. The ordinary method employed in timing races, namely, the use of a stop-watch, is not very accurate, since it depends upon the human observer whose readings are liable to error. Without great elaboration, moreover, it would not be possible with stop-watches to time every 10 yards throughout a 220-yards race. At present we know only the *total* time taken by the champion runners over the whole distance. It would be of the greatest interest to find out how rapidly they start, how soon they reach their greatest speed, and how the speed falls off as they fatigue. It is simple and comparatively inexpensive to employ electrical timing for the purpose. Plate XXIV, *a* shows the running boards of the winter track at Cornell University with a series of coils accurately placed at 1, 3, 6, 10, 15, 20, 30, 40, 50, 60 yards respectively from the starting point. These coils (each of about 200 turns of insulated copper wire) are connected up in series with a galvanometer in the pavilion, arranged to record its movements photographically on moving bromide paper in a camera similar to that used with the string galvanometer. A runner carries a thin magnet (Plate XXIV, *b*) tied round his waist: the one shown in the plate is nothing but a hack-saw blade, with its teeth ground off, and magnetised in a solenoid; it is light and flexible and it does not interfere with the runner in the least. Each time he passes one of the coils the magnet induces a current in it, which is recorded on the bromide paper in the camera, as shown in Fig. 53. Two records are given in the

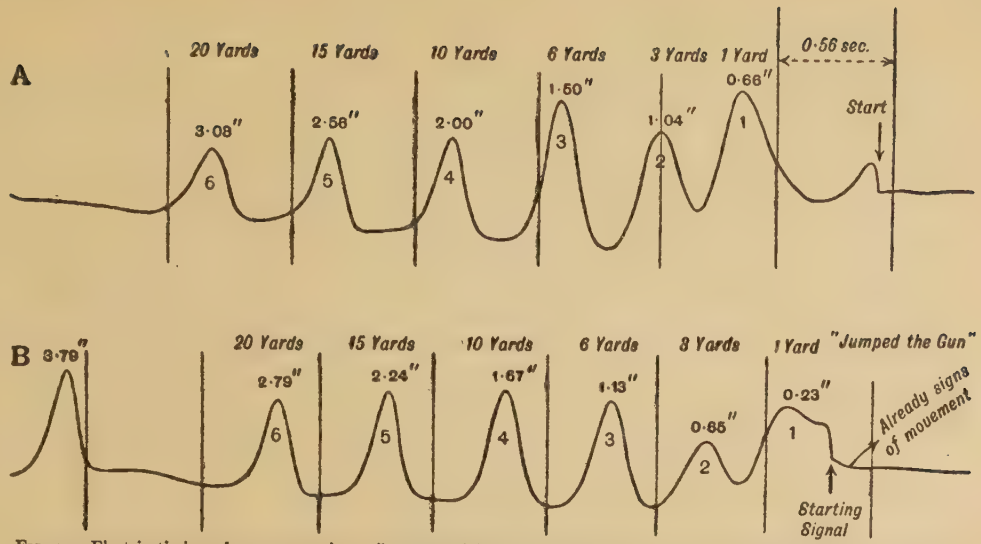


FIG. 53.—Electric timing of runners passing coils arranged by the side of the track and carrying thin steel magnets on their vests.

figure both reading from right to left. The upper is of a runner capable of covering 100 yards in 10 secs.: the lower of another runner, not so good as the first, who "jumped the gun" at the start, so was 0.43 sec. ahead of the first at one yard, and 0.29 sec. ahead at 20 yards. A typical set of observations on X (a fairly good runner, see Plate XXIV, *b*) and Y (a fairly bad one—the author) is given below.

Distance: yard	1	3	6	10	15	20	30	40	50	60
Time: secs. X	0.65	1.07	1.56	2.10	2.72	3.28	4.36	5.42	6.51	7.56
Time: secs. Y	.80	1.28	1.82	2.42	3.07	3.73	4.91	6.06	7.22	8.37

It is obvious that by such means as this we can analyse the process of sprint running to an extent never before possible. The times can be read to $\frac{1}{100}$ sec., or even to $\frac{1}{200}$ sec., with accuracy. The arrangement costs not much more than $500 to rig up and should give results of permanent value in studying athletes and athletics. Anyone with a little electrical knowledge can work it, and the cost of maintenance is little more than that of the photographic paper used.

It is not necessary that the coils should be at the side of the track: they might be suspended from above. Each of six runners might be timed at the same moment, by employing six sets of coils, together with the six strings of a galvanometer such as was used for sound-ranging during the War. Such an arrangement if used at the Olympic games would give results of quite extraordinary interest.

LECTURE VII

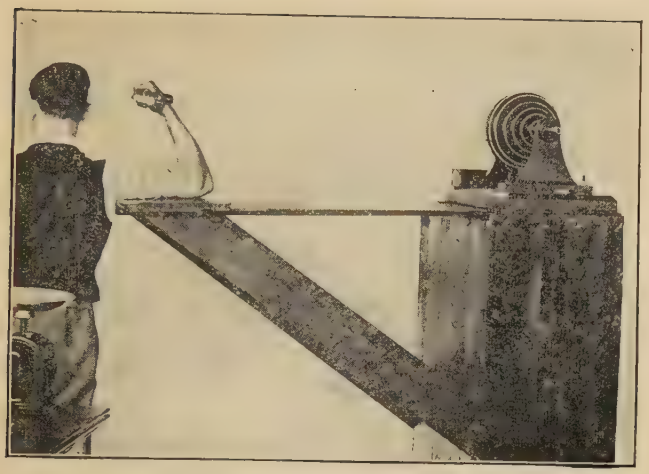
Physiology as a Meeting Ground of the Sciences

A SCHOLAR of the seventeenth century, Dr. Wallis, records—to quote his words—that about 1645 when he lived in London he had "the opportunity "of being acquainted with divers worthy persons, "inquisitive into natural philosophy and other "parts of human learning and particularly of what "has been called the new philosophy or experi- "mental philosophy. We did, by agreement, di- "vers of us, meet weekly in London on a certain "day to speak and discourse of such affairs. Our "business was to discourse and consider of phil- "osophical enquiries and such as related thereunto, "as physick, anatomy, geometry, astronomy, navi- "gation, staticks, magneticks, chymicks, mechan- "icks, and natural experiments. We then dis- "coursed of the circulation of the blood, the valves "in the veins, the venæ lactæ, the lymphatick ves- "sels, the Copernican hypothesis, the nature of "comets and new stars, the satellites of Jupiter, "the oval shape of Saturn, the spots on the sun, the "improvement of telescopes, the grinding of glasses, "the weight of air, the possibility or impos-

"sibility of vacuities and Nature's abhorrence "thereof, the descent of heavy bodies and the degree "of acceleration therein." These worthy and inquisitive persons later continued their meetings elsewhere, forming the Philosophical Society of Oxford, the original minutes of which are still preserved there. So great was the variety which a small body of learned men of the seventeenth century could discuss.

Even in the nineteenth century Helmholtz, starting as a surgeon in the Prussian army, was able to become one of the foremost applied mathematicians in Europe, three times professor of physiology, finally professor of physics and director of the Physico-Technical Institute at Charlottenburg. His investigations occupied physiology, physiological optics and acoustics, chemistry, mathematics, electricity and magnetism, meteorology and theoretical mechanics. He wrote also on philosophical and æsthetic problems. Even at this short distance it is difficult to imagine a modern scientist capable of covering effectively even a fraction of his field.

With the progress of knowledge and the advance of science the forming of arbitrary divisions between the different branches has become inevitable. Watertight compartments are not in themselves good things; but when science and scientific departments have to be organised on the scale of the present day,



(*a*) A man pulling on a flywheel designed to measure maximum work in a muscular contraction. The work is done almost entirely by the biceps and brachialis anticus muscles (*cf.* Plate VIb), (p. 196).

(*b*) An experiment at Queen's Club, London, showing a measurement of the oxygen consumption of the subject A, referred to on p. 221.

(*a*) The track at Cornell University, U.S.A., with timing coils to record the speed of runners (p. 230).

(*b*) A runner carrying a magnetised strip of steel across his body, by which currents are induced in the coils (p. 230).

certain arbitrary administrative divisions are necessary: otherwise science would totter under its own weight. We must not imagine, however, that because the names are different, and different for reasons of expediency, the things themselves are different too. Words and names are an essential part of our methods of thought and action, but we must continually seek to avoid the unspoken, implicit, often unrealised, assumption that when the names are the same the things are necessarily the same, when the words are not the same the things themselves are different. It may be necessary to organise our scientific departments behind visible boundaries; but the wise man will remember that, in respect of scientific progress as in other things, parthenogenesis is rare in Nature and generally two parents are necessary before a new individual can develop. It is often fruitful to apply the methods, outlook and discipline of one science to the problems of another. Without fertilization from outside a science may remain sterile.

What I shall say, therefore, about physiology is true not only of physiology: all sciences should provide meeting grounds for all the others. Of physiology, however, it is particularly true that progress comes mainly from without. Such a thing as "pure" physiology can scarcely be imagined. Physiology is a game for beggars, explorers and adven-

turers: living by their wits, trusting to their skill in mastering unexpected difficulties, relying on the good will and knowledge of others, guarding always against the tricks which the living cell will try to play upon them, they must be prepared to use any and every means for studying the mechanisms and principles of life. It is said to be possible for a man to be a "pure" mathematician, it has even been rumoured that a man may be a "pure" organic chemist: such a state, if indeed it exist, must be a lonely and unhappy one, at least for ordinary folk. In other branches of learning, and in physiology particularly, such a state of isolation is impossible. Physiologists must try to be physicists, chemists, zoologists, anatomists, physicians, surgeons, pharmacologists, mathematicians, even philosophers and sociologists, and the more of these trades they can practise the better. They are amateurs admittedly, Jacks of all trades and masters of none, but that is the price exacted by the attractive mistress whom they serve.

Physiology is the study of the mechanisms of life. Mechanisms indeed they are, like those of the engineer, though smaller and more subtle. They take in and they give out energy: they do mechanical work. They obey the ordinary laws of physics and dynamics. They are governed by the rules pertaining to systems with many independent variables.

They occur in a heterogeneous system of aqueous solutions and suspensions, maintained in a state of dynamic equilibrium: they depend upon the structural and physical chemistry of the bodies involved. They possess an inherited organisation, a capacity for growth, maintenance and repair, and an obvious "purposefulness" and "function" which are unknown in physics and chemistry, but are real enough things and are the special objects of study of the biologist. However much we emphasise the physical and chemical features we cannot neglect the fundamental biological background of the picture. In such studies one needs to know something about the structures, gross and microscopic, which make up the organ or animal: this implies anatomy and histology. And finally in searching for experiments to elucidate the mysteries of life we cannot neglect those gigantic, wanton and often gruesome experiments which Nature herself makes upon men and animals in disease: Nature is not an anti-vivisectionist. One has only to remember the discovery of insulin to realise how important to physiology may be the indications of medicine and pathology. Scarcely any science therefore may not be invoked in the study of the processes of life.

In saying that physiology is the meeting-ground of the sciences I would indicate something more than the obvious fact that physiology needs all the other

sciences for her proper development. I would assert that in bringing the other sciences together, in order to use them for her own ends, physiology is really serving, not only herself but them. Zoologists, physicists and chemists may find enlightenment sometimes in the methods and results of physiology; sociologists and economists might seek instruction in the organization of living units into an individual whole: and in any case physiology deals objectively with the fundamental basis of all the other sciences, namely, with the mechanisms of perception, life and thought, matters which lie at the root of all natural knowledge. Incidentally because of the special nature of her problems, dealing with units—*viz.* living cells which are somewhere, in size, between those of the engineer and those of the atomic physicist, and with material of a particularly difficult character, physiology has developed methods of experimental attack which are, in many respects, superior to those of other sciences. Thus in pointing out how much physiology is already indebted to other sciences and how much she intends still to gain from their help, I shall avoid undue modesty on her behalf, and shall make the broad claim that in some respects other sciences too have much to learn from her. She is a very desirable neighbour: no school of scientific thought is complete without a department of general physiology.

The place of physiology among the sciences is an important practical matter. Physiology has been called the "handmaiden" of medicine: I would call it rather the "spiritual adviser of medicine": certain, however, it is that physiology is an essential part of a liberal medical education, not so much for its immediate practical results (though these are sometimes considerable enough) but for the contact which it makes between medicine and natural science. If a physician has been taught to think and investigate in terms of the normal living cell or body, he will have more basis for observing, studying and treating it when it goes wrong. The place, indeed, of physiology in medicine is universally recognised, and a school of physiology exists in all well regulated medical schools.

Here lies a danger: for various reasons of expediency medical schools are often removed from universities: they must go where hospitals are needed, to the areas of densest population, while the universities themselves—for equally good reasons—remain outside. Thus there is a tendency for physiology to be divorced from universities, to be cut adrift from nearly all the sciences on which it depends; which is disastrous to physiology and a serious loss to those other sciences. No well balanced university can afford to be without physiology among its scientific departments; and if it be necessary to re-

move the main department of physiology to a distance, with the medical school, pains should be taken to ensure that in the university itself, right in the middle of the other scientific laboratories, there should be a vigorous school of "general" physiology, where the more scientific and philosophical aspects of the subject shall be taught and investigated. Only by such means can the fundamental study of life be properly pursued: only by such means may the other sciences be kept in mind of the gravest of scientific problems. For of all things, surely, the objective study of life itself is worthy of the attention of scientists and philosophers.

The most essential fact about a living creature is that, with the properties of matter as they are, units possessing the type of organisation which we call "life" are possible only within certain limits of size. They are dependent on such factors as diffusion, for their provision of material, on surface forces and organisation for their structure; and these would not work in the way required in systems of more than microscopic size. For this reason the ultimate unit, the cell, is very small, and we find ourselves almost incapable of dealing experimentally with single units. This is no longer strictly true; in recent years Robert Chambers of New York has devised methods of microscopic manipulation by which, for certain purposes, single cells can be dealt with ex-

perimentally; and in a very different direction Adrian of Cambridge has, with an 1800-fold valve-amplification, succeeded in recording the electric action-currents of a single nerve-fibre. In general, however, the statement holds, and for the most part as physiologists we are concerned with large numbers of independent living units, each with a mass of the order of a millionth of a milligram: far larger than an atom or a molecule, far smaller than any other organised machine. Equally, in its ultimate physical and chemical processes the cell is intermediate between these two. The fundamental reactions of the living cell, occurring in aggregates of a large but finite number of molecules, take times measurable say in ten- or hundred-thousandths of a second and not in the millionths, or million-millionths, that the atomic physicist employs. All our phenomena are upon a certain scale of size and time, and this entails a certain method of thought. Physical effects, which to a chemist or an engineer may seem of no importance, and which to the atomic physicist have passed out at the other end of his spectrum, are to us matters of fundamental necessity. To see the problems of physiology in their true perspective one needs to be acquainted with the theory of dimensions and to apply it occasionally to the animal and cell.

Borelli, the author of *De Motu Animalium*, living in the seventeenth century, was a professional math-

ematician and attempted to apply mathematical methods to the study of the living animal. In particular he investigated the mechanics of muscle, and his book is filled with pictures of levers, pulleys, muscles, bones, birds, fishes, and even men in diving suits! The measure of success that attended his efforts led his less cautious followers to generalise the applications which he made by hypotheses (those of the iatro-mathematical sect as they were called) which hindered, rather than advanced, medical science. Knowledge, in his time, of the actual facts was insufficient to justify any widespread attempt to apply mathematical reasoning to the study of life and especially to the art of healing; for out of mathematics it is not possible to obtain more than one puts in! Even today physiology is still in the state that physics was in at the time of Joule, when the advance of electrical knowledge required rather the careful establishment and measurement of actual units and phenomena than any far-reaching hypotheses about their nature. The acquisition of quantitative data in physiology is very difficult (if we insist that the data shall be accurate) as compared with the amassing of similar facts in the "exact" sciences. The variability of tissues, and the fact that any kind of interference with the living cell is apt completely to distort its functions, hinder us from obtaining the accuracy and consistency which we require, if the

results are to be capable of mathematical interpretation. In some directions a mathematical treatment is already possible. Helmholtz in his work on the senses was able to find effective scope for such methods, and of course a statistical treatment of the problems of biology is capable of leading to certain types of results, and of describing certain general tendencies, such as no other methods can give. For a description of the average behavior, and of the general causes underlying gross phenomena, such mathematical statistical methods are valuable and necessary, though they cannot replace accurate observation: and a certain acquaintance with them and with the theory of errors is essential to anyone who wishes to deal with systems such as those occurring in biology, which contain large numbers of units often of very variable nature. As regards, however, the more intimate things, the ultimate physical and chemical causes and relations of life phenomena, other methods are required.

The rôle therefore of mathematics in physiology is a limited one. A knowledge of mathematical methods enables one indeed, with more confidence, to use the tools, physical and chemical, which other sciences provide. The theory of excitation of the nerve by an electric current, essentially a physico-chemical theory, requires the aid of differential equations and of Fourier series for its proper application. The

analysis of the heat-production of muscle and nerve demands an elimination of the effects of flow of heat and of the mechanical properties of galvanometer systems, which can really be attained only by the numerical solution of an integral equation. To take another example, in a recent attempt, by a colleague of mine in London, to measure the amount of light absorbed from the rays of the sun by the human skin, it was necessary to solve the problem of how much radiation is picked up by a circular disc from another circular disc, parallel to it, on the same axis and uniformly illuminated. This problem I lightly told my friend was probably a simple one and I would try to solve it for him. Actually I found it to be completely beyond my limited powers: it took two distinguished professors of mathematics several hours to arrive at a solution! Continually in dealing with physical apparatus or with physico-chemical effects an employment of mathematical reasoning becomes necessary. The mathematician, however, has a place in physiology only in so far as he is also acquainted with chemistry, physics, or the methods of statistical mechanics. A mathematical training, naturally, is of great advantage to a worker in this, as in any other science. Apart from the faculty of dealing quantitatively with things, apart from the power of being able to appreciate physical or statistical methods and to understand the theory of instruments,

or of dimensions, the discipline of a mathematical education is of value to anyone who has to deal with complex and involved effects and reasoning; and the habit of precise statement and formal proof which a mathematician acquires will be of the greatest value to him—and his colleagues—when he comes, in whatever science, to try to explain his results either to himself or to others. One of the gravest difficulties of science today is the load of badly digested work which burdens its literature.

I mentioned the theory of dimensions. It is strange how that method of approach, based apparently on simple mathematical logic, may sometimes give a clue to important physical facts. During the late war a young naval lieutenant, now a distinguished mathematician, working at the problems of ballistics, was reflecting on the formula generally employed by gunners for expressing the air resistance to a moving shell. At low velocities the formula is simple:

$$F = \rho v^2$$

F having the dimensions of a pressure, ρ being the density of the air, and v the velocity of the shell through it. At high velocities this simple law is no longer obeyed: the resistance increases more rapidly than the square of the velocity, and it was common to express it in the form

$$F = \rho v^2 f(v)$$

where f(v) is some function of v, unity at low velocities, greater than unity at high ones. Now this formula offends a mathematician's sense of propriety. F is a pressure, so is ρv^2, f(v) therefore is a mere number of no dimensions. How could a function of a velocity be made a number of no dimensions? Obviously only by dividing the variable velocity v by another unknown and constant one a, so that the formula should be written,

$$F = \rho v^2 f(v/a)$$

Merely a matter, one might reflect, of mathematical correctness: one that a college "don" might worry about, but of no great concern to serious people like gunners. But wait: what value could be taken for *a:* obviously there is only one velocity characteristic of air, *viz.* the speed of sound in it: *a* must clearly be the velocity of sound. Yes, but the velocity of sound is not constant, it depends upon the temperature: and at long ranges shells go high in the air, to heights where the temperature, and therewith the velocity of sound, are considerably less than on the ground. Thus the correction to the simple formula

$$F = \rho v^2$$

obviously must depend, not only on the velocity of the shell itself, but on the temperature (as distinguished from the density, which was already taken into account) of the air through which it passed. The new correction was experimentally applied,

certain well known and important, but mysterious anomalies in the ballistics of long-range guns were explained, and the correction was adopted "into the Service." A strange and interesting sequel to a bit of mathematical pedantry quite unworthy of a Lieutenant in The Royal Naval Volunteer Reserve!

Let me take an example from physiology, to illustrate how the sciences may be intermingled. Imagine a series of animals to exist, similar in all respects except size. The weight of an individual in the series will vary as the cube of its linear dimensions: the cross section of its limbs, however, will vary only as the square: it is a common problem in engineering: soon a limit will be reached beyond which an increase in size will result in shearing or crushing stresses too great for the animal's structures to bear. Either he must perish, or his design must be changed. We cannot imagine a spider, with long thin legs spreading out horizontally, to attain the mass of an elephant. He would surely break under his own weight. We cannot picture an elephant of ten times the linear dimensions of those which actually exist: the whole of the space beneath his body (and more) would have to be occupied by legs in order to stand the pressure of his weight! Or consider quickness of movement, and assume that a series of similar animals of different size are endowed with exactly similar muscle-fibres, which can contract and

shorten at the same speed. This is a very natural assumption—microscopically, and in every way we can observe them, the muscles of similar animals are indistinguishable. Our assumption is, in other words, that these animals, of different size, can produce similar movements the same number of times per minute: or that they can produce the same angular velocities in their limbs. Now the mass of a limb varying as the cube, and its linear velocity as the first power, its momentum will vary as the *fourth* power of the dimensions of the animal. This momentum is produced or destroyed, during rapid muscular effort, by forces on tendons, muscles, joints and bones: the strengths, however, of these structures are only as their cross-sections, *i.e.* as the *squares* of their linear dimensions. Consequently the stresses increase much more rapidly than the strengths of the structures which are required to stand them: obviously an impossible condition, for it would lead to continual breakage in the larger animals. Clearly our hypothesis that the muscle-fibres of the different animals are similar in their time-relations is impossible: the larger animals must somehow be endowed with muscles which contract and shorten more slowly.

We can look at the matter in another way—the kinetic energy of a limb in such a series of animals, on the assumption of similar muscle-fibres, would vary as the *fifth* power of the linear dimensions,

while the total work—being proportional to the mass of the muscles—would increase only as the *cube*. A greater and greater fraction of the mechanical energy of the muscles would be used in accelerating the limbs themselves, as we passed to the larger animals of the series: a most inconvenient and wasteful arrangement. Indeed one can deduce, from principles of dimensions alone, that a series of athletic animals of similar design but of different size ought all to be able to move with the same maximum *linear* speed, or to jump the same height. This is more or less what we find: a whippet and a racehorse are not unlike in design, and they have nearly the same maximum velocity: a cat and a tiger are not dissimilar, and in running or jumping there is not the many-fold difference one might have expected from their relative sizes. The small animal makes up for shortness of stride by greater frequency in movement.

Consider further a series of similar animals of different size, endowed (as we have shown) with the same maximum linear speed. Each time that a movement is made kinetic energy is developed and degraded in the limbs, to an extent proportional (if the linear velocity be constant) to the mass of the limb moved. Now in the smaller animal the movements will be more frequent, more energy per unit of body weight will be wasted in a given time in go-

ing at a given linear speed, the animal will become more rapidly fatigued. Thus, unless the design be changed to one involving relatively lighter limbs in the smaller animals, these though having the same maximum speed will tire more rapidly: unless (and this also tends to happen) they can develop, owing to their smallness, a greater relative flow of blood to supply themselves with oxygen and energy.

Such applications of the theory of dimensions might seem to bear rather upon the problems of general biology than upon the more specific and intimate questions of physiology. Let me illustrate again how arbitrary are boundaries between the sciences. How is it that a fly is able to move its wings several hundreds of times a second, while even we, and how much more the elephant, find it difficult to carry out the same number of movements in a minute? Granted that the theory of dimensions proves that the larger animals *must* move more slowly, if they are to survive, while the struggle for existence has ensured that most animals move as rapidly as they dare: what is the *mechanism* by which this adjustment of speed to needs and dimensions is brought about? Is it nervous—are the muscles in different animals intrinsically similar in their time relations, but caused to shorten at different rates under the influence of the nervous system? Recent physiological research insists that this would

be a very wasteful adjustment in the larger animals. One's "biological" sense would be offended by such an uneconomical arrangement, and in point of fact, on further investigation we find that the adjustment is in the muscle-fibre itself. In the physical and chemical events which follow a stimulus the scale of time in one muscle-fibre may differ widely from that in another from an animal of a different size. The formation of the new molecular arrangements, the liquid crystals or whatever they be, which occur in muscular contraction, proceeds at a rate depending upon the biological needs of the animal to whom the muscle-fibre belongs. Here is a mechanism—the physico-chemical mechanism of the muscle-fibre—of great importance, widely studied in the last few years, found to be admirably suited to the biological needs of the animal; and its discovery and description in physico-chemical terms were largely suggested by an application of the theory of dimensions to a hypothetical series of similar animals of varying size! Could one want a better example of overlapping sciences—mathematics and the theory of dimensions, biology and a faith in the adaptability and economy of the organism, the mechanics and thermodynamics of movement, the chemistry and physics of a crystalline liquid—all leading to a new Chapter in the Physiology of Muscle!

Turning next to another science—physics—it is

interesting to inquire exactly what rôle physics should play in the investigation of life-phenomena. All these phenomena occur in an aqueous solution, so that, adopting the usual nomenclature it is physical-chemistry, rather than physics, to which the physiologist should appeal. It happens, however, that many of the phenomena of life and activity are rapid, fugitive and complex and it needs often unusual experimental means to measure them accurately. For example, the electric change which occurs in a nerve when stimulated is only a few thousandths of a volt, it reaches a maximum within a fraction of a thousandth of a second, and the whole wave has gone by in a few thousandths. No ordinary method employed by the physical chemist will even detect such a wave. Nothing but a kathode-ray oscillograph and valve amplification are capable of giving a true time-record of it, and yet our knowledge of nerve depends very largely on a correct description of the electric changes which occur in it—for there is very little else we can measure or even observe. The initial heat-production in a nerve, when an impulse travels along, is of the order only of one ten-millionth of a degree. Measuring this small quantity of heat, and giving it its proper position in time relative to the impulse which started it, are processes involving the most delicate of electrical instruments. The string-galvanometer, used for recording the

electric changes of muscle, nerve and heart: x-rays for studying movements of heart, lungs, and digestive tract, for producing sterility, and some day—one hopes—for analysing the crystalline nature of living protoplasm: and all the countless instruments for studying the sensations, for measuring the reactions, and for recording the energy exchanges of the animal: to devise and to use all these require the training and experience of the physicist. With the quantum theory we have not yet seriously to deal—though we are coming perilously close to it with the spectra of hæmoglobin and its allied substances; with the theory of relativity we have not even begun to meddle—though I suppose we shall some day. With such problems, however, as the conduction of heat and electricity, as diffusion, surface forces, molecular arrangement at surfaces and interfaces, or in the structure of the cell, we are greatly concerned, though these things, working as they do in a heterogeneous system suspended in salt water, one is more inclined to relegate to the domain of physical chemistry. With pure physics we are concerned rather as designers and makers of instruments, and the fleeting nature of the phenomena they have to observe and record has made some physiologists very apt in dealing with such physical problems: so that when a physicist, or a chemist, requires a rapid and sensitive galvanometer, a well

designed lever or an optical system for recording sudden movements, he remembers, if he is wise, to come and take advice from the physiologists.

With certain physical principles of course, such as the laws of thermodynamics, physiology is much concerned. Contrary to what some, on very imperfect evidence, have supposed, all the usual laws of physics, including the principle of the conservation of energy, hold in the economy of the living cell; even the second law of thermodynamics, based as it is on the properties of large numbers, appears—so far as one is able at present to detect—to apply exactly to mechanisms of the size of the cell. It might not have applied: the living cell, by a capacity for sorting molecules, might have proved to be a "Maxwell's demon". Many have speculated about the subject but with little avail. It would be amusing, if a living cell should prove to be the only means of diminishing the entropy of the universe, but I fear there is little hope of such a seven-day wonder!

Of all sciences, chemistry is the one which has the most obvious bearing on the study of the phenomena of life. These occur in a system which consists, essentially, of dynamic chemical equilibria existing in a heterogeneous chemical medium. It is obvious that most of the things which happen inside a living cell are of a chemical nature—indeed it is difficult to suggest any which are not. In recent

years the importance of chemistry to physiology has been very fully realised and in many places in England and America, and indeed all over the world, departments of biochemistry are springing up. These have very different purposes and organisations. Some are closely allied with physiology and maintain the biological standpoint. Others proudly assert a complete indifference to their parent, and emphasise rather the chemical than the biological outlook. Some study vitamins, metabolism, internal secretions, the specific action of drugs: others emphasise rather oxidation-reduction potentials, colloidal reactions, ionic activity, and other important chemical building stones of the biological edifice. Biochemistry is so important that freedom is essential, but one hopes—for the future of the subject—that it will not be too proud to agree to a treaty of mutual co-operation with its parent.

One has only to look over the pages of a book of physiology, or to reflect on recent discoveries in physiology and medicine, to realise the extraordinary importance of the rôle of biochemistry. Consider the hormones; the suprarenal glands secrete into the blood a chemical substance—adrenalin—which if of great importance to the animal, which is intimately concerned in the activities accompanying struggle, excitement or emotion, and which has been given a chemical formula and synthetised in the

laboratory. The thyroid gland is an essential organ for normal health; its disturbances,—hyper- or hypothyroidism—lead to painful abnormalities, and the active substance which it makes—thyroxin—has been isolated by Kendall at the Mayo Foundation at Rochester, Minnesota, and shown to possess qualities of extraordinary potency in affecting the resting metabolism—the total balance of oxidative breakdown—in man and other animals. Harrington at University College, London, has recently devised better means of extraction, by which ten times the yield of the active agent is obtained from a given amount of gland. For long the chemical nature of thyroxin has remained a mystery. A few months since Harrington announced the discovery of the structure of its iodine-free derivative, together with its synthesis. Later he and Barger revealed the full story, iodine and all. Dakin independently has done the same thing. Another complete victory of biochemistry has been recorded. It is a difficult, long and laborious art, and more "messy" than the pursuits of the pure chemist, this isolation of active agents from living glands and tissues: but it is a necessary part of the war that goes on in biochemical laboratories: and occasionally come great and glorious victories which echo round the world and hearten men for further struggle.

When the substance has been isolated there still

remains the task of the organic chemist, its description in a structural formula and its synthesis. Even then, however, we have only begun. Its synthesis by the cell is certainly different from its synthesis in the laboratory, and abnormalities in its production in the living body must depend upon its manner of synthesis in the cell. Furthermore, with the most exact description even of that, its specific action in the body cannot be understood until we have a knowledge of its intermediate metabolism, a description of the chemical structure of the living cells with which it acts. In no single case has this degree of knowledge been reached. Take the case of insulin, the absence of which from the circulation and organs causes diabetes—the continuous excretion of sugar, leading in extreme cases to coma and death. This substance was isolated by the workers at Toronto; its formula is not yet known, but there can be little doubt that in the future, near or distant, it will be described and synthesised like adrenalin or thyroxin. It is concerned with the metabolism of sugar, and in order fully to understand its behaviour it will be necessary to know more than at present we know about the nature of the sugars, their chemical constitution, and the constitution of their allied substance glycogen. Thus the work of Irving and his school at St. Andrews, Scotland, is a very essential means to progress in our knowledge

of carbohydrate metabolism in the body, and its abnormalities.

There are many other obvious problems to which biochemistry must some day afford an answer. The extraordinary efficacy of the vitamins in preserving the body in health is well-known: minute traces of them are sufficient: some of their properties are known: but at present we have little clue as to what—if indeed they be definite chemical compounds at all—their chemical constitution is.[1] Again it has recently been realised that pernicious anæmia can be treated effectively by feeding the patient continually with liver: what the cause may be of the relief effected by this means remains at present a mystery: another chapter in biochemistry has been opened, and no one knows where or how it will close.

These are obvious illustrations. In the intermediate metabolism of the body many chemical substances of known composition, and still more of unknown composition, occur. The body is in a state of dynamic equilibrium: substances are passing through a machine: occasionally we can stop the machine and get some of the intermediate substances out, often, however, they must pass so rapidly

[1] Since these lectures were given it has appeared that Vitamin D can be made from ergosterol by ultra-violet light. One ten-millionth of a gram per day will prevent rickets in a rat.

through that they cannot be stopped and we do not realise even their existence. Sometimes errors of metabolism turn up, which throw some light on these problems: witness the rare disorder which occurs in families and is known as "alcaptonuria". In this condition, which is congenital and lasts throughout life, the urine darkens considerably when made alkaline and exposed to air. This is due to the presence in it of a substance known as homogentisic acid, dioxyphenylacetic acid, the amount of which bears a constant ratio to the total nitrogen excreted. Something has gone wrong permanently in the usual chain of processes, some "hand" in the factory is missing, and a by-product has appeared which normally is either absent or exists only for such a short time that its presence is undetected.

It is impossible by ordinary chemical methods to follow the reactions which go on inside the living cell. We can only work by isolating chemical substances, breakdown products in one place, intermediate products in others, studying the relations that exist between the chemical substances that go in and those that come out, and so endeavour to interpret the mechanism. It can be imagined that if one were forbidden to enter a drug factory and were permitted merely to study the substances that went in and those that came out, to witness the changes in those substances when a member of the

staff went ill, perhaps to poke a rod through a window sometimes and to see what one got out on the end of it, under such conditions one would find it difficult to describe all the processes that went on within the walls. That is the kind of problem biochemists have to deal with and it is one where chemical knowledge and a high degree of chemical intuition are essential.

Chemistry, however, in these problems is not all; a knowledge of biology is equally necessary, for animals work in certain ways, and above all the chemist who comes to physiology needs to be ready to turn up his sleeves, to become a Jack of all trades, to use any methods or tricks, however unorthodox, in order to get a clue as to what is going on. The chemist who comes to physiology must not be proud. He must not mind, if the need arises, pushing a stick through the window and tasting whatever he finds on the end of it when he draws it out. There is enormous scope for organic chemists—if they be sufficiently adaptable—who come to physiology, to study the chemistry of the substances and processes which make up the dynamic equilibria of life.

A striking example, and one to which I have often had occasion to refer in these lectures, of the essential nature of the evidence which chemistry can bring to the study of vital processes, is that of lactic acid in muscles and other tissues. For many years

physiologists had studied muscular fatigue. Rather more than a quarter of a century ago Fletcher, working on their respiration, realised the importance of oxygen in the recovery of muscles after activity. A few years later, in collaboration with Hopkins, he discovered that all the phenomena of fatigue, rigor and recovery were to be attributed to the formation, and to the removal in the presence of oxygen, of lactic acid. This classical work of Fletcher and Hopkins has inspired all the researches which have been carried out since on the physiology and biochemistry of muscular activity: a vast and inspiring edifice has been reared on their foundation, and in all kinds of directions the knowledge gained has been found fruitful. Today the formation of lactic acid during activity or in the absence of oxygen, and its removal in the presence of oxygen, are recognised as almost universal phenomena in the life-processes of animal cells: according to Warburg, the most essential biochemical characteristic of carcinoma tissue, is an abnormality in this chain of reactions. And the whole structure arose from the collaboration of a physiologist who really knew a good deal about muscles with a biochemist who was really capable of studying their chemical relations accurately.

The work of Ehrlich has shown the importance of therapy by specific substances. Synthetic drugs,

such as salvarsan (606), or Baeyer 205 which is specific for sleeping sickness, or plasmochine which is specific for malaria, are certain to find considerable application in the medicine of the future. The control of the body by specific chemical means is still only in its infancy and success requires the co-operation of people with first class skill both in organic chemistry and in pharmacology and physiology. The smallest changes in a chemical molecule may be of ultimate importance in this connection. Molecules whose formulæ may be almost indistinguishable may prove quite different in their effects on the body. One optical isomer may be active, the other completely inactive: a few milligrams of hen's egg-white may cause immediate death to an animal sensitised to it, while the same animal may stand a gram of duck's egg-white without turning a hair. The nature of such differences is a matter of organic chemistry, tempered, however, by a certain knowledge of biology. The "pure" chemist or the "pure" biologist sees such things flat: one needs both sciences for stereoscopic vision.

In another direction, namely on its physical side, chemistry is a necessary tool to the physiologist, an essential page in his philosophy. He is dealing with equilibria: sometimes these are ordinary balanced reactions, as in the case of the combinations of hæmoglobin with oxygen and other gases; sometimes

they are rather of the nature of steady states, dynamic equilibria, where the level of a pool is kept constant by water pouring in and out at the same rate. In living cells there are many genuine reversible equilibria; ionic ones, especially those concerned with the hydrogen ion; chemical ones, such as the reaction of oxygen with hæmoglobin; heterogeneous ones, such as those coming under the heading of adsorption. Differences of electrical potential exist between the insides and the outsides of the cells, which are a sign of inequalities in the distribution of ions on the two sides. Surface phenomena, electrical double layers, the colloidal behaviour of proteins, all tend to come under this category. On the other hand in mechanisms of the minute size of living cells, diffusion which works so sluggishly in the case of great systems becomes very rapid indeed. Diffusion in the living cell is the only, or almost the only, process by which chemical interchanges can occur between the interior and the environment. From diffusion we are led to consider the velocity of chemical reactions which never reach an equilibrium. Many chemical reactions as we study them in laboratories are apparently rapid; a rapid chemical reaction is one whose speed is great compared with that of the factors at work in bringing the reacting bodies into each other's neighbourhood. On the large scale, mixing and diffusion are

usually so slow that any lag observed in reactions must lie at their door. In the living cell, however, the dimensions are so small that reacting bodies can be brought into one another's presence with great rapidity, and the actual velocity of chemical combination must in many cases be the weakest link in the chain. The most fundamental of all these problems of biochemistry is that of the actual mechanism of its reactions, the path by which change takes place, the nature of the intermediate compounds. It is well known that in living cells reactions may lead to different results from those produced by ordinary chemical methods. The organic chemist has much to learn from the effectiveness and economy of biological synthesis and breakdown. In the living cell reactions may seem to be rapid, but compared with the extreme rapidity with which diffusion can go on, with which the reacting bodies can be brought together or removed from one another's presence, they must be regarded probably as being in many instances exceedingly slow. If there were any physical means of removing an intermediate product, for example a greater diffusion constant or a greater solubility, then intermediate products might be torn from the cauldron of chemical change and dealt with along quite different paths from those which are decided simply by the laws of chance prevailing in homogeneous mixtures.

A study, therefore, of the actual mechanism and the velocity of chemical reactions, even when rapid, and of the factors that affect them, is a very necessary means to the study of the processes of the cell. Recently Hartridge and Roughton at Cambridge, England, have examined chemical changes which are complete in a few thousandths of a second, and there would seem no reason why an extension of their methods should not be made to many other types of process. If so, with a knowledge of the relative importance of different physical factors, in a mechanism of ultra-microscopic dimensions, we may hope gradually to arrive at some idea of the dynamic equilibrium which exists inside a cell.

Living matter is arranged in a sense as a crystal is. X-ray analysis has revealed an organised molecular structure in naturally occurring fibres. Doubly refracting portions are visible in a muscle at rest undergoing no strain. Such double refraction implies the existence of a molecular structure, a crystalline form in the liquid medium of the cell. Recent work of Adam and others, on the orientation of molecules in surfaces, strongly urge us to regard the interfaces that are known to exist in a living cell as the site of molecular organisation. Other phenomena lead us in the same direction. Recent work on the so-called "viscous-elastic properties" of muscle, in which a very definite hysteresis is found to occur

which is not due simply to ordinary viscosity, has made us look for an analogy which again has been found in molecular arrangement. The apparent viscosity of muscle may be increased twenty times by a stimulus: it is difficult to attribute such an enormous change to a simple alteration of crude viscosity in the colloidal solution permeating the structures of the cell. Much more likely would seem the hypothesis that the protoplasm has an organisation analogous to that of a crystalline liquid, and that excitation causes a change in that crystalline condition with a rearrangement of the molecules. Such molecular rearrangements are known to take place, as Adam has found in several cases, with a considerable time-lag, which in such experiments as these on muscle would necessarily appear as simple viscosity. This apparent viscosity is not confined to muscle, it is a property of most fibres that are (or were at one time) alive, indeed of protoplasm and its products. In the molecular arrangement and organisation of protoplasm, as it were in a kind of supermolecular structure, we must expect to find the clue to much of the behaviour of the biological unit.

There are many physico-chemical phenomena well-known in physiology, of which no explanation can, as yet, be given. The extraordinary specific effect of certain ions, the fact that to the heart potassium

is utterly different from sodium, the extreme potency of the ions of the rare earths, the amazing capacity of the body for regulating its hydrogen ion concentration, all deserve a very special mention as phenomena where physiologists need a physical chemist to help and advise. Not only, however, to help us but really in a sense to help himself, for in these very obvious things he will get away from abstractions, and see for himself things of extraordinary vividness and apparent simplicity which are at present complete and absolute mysteries. What is more exciting than to witness something which one is utterly incapable of understanding? It is as though one became a child again and went to see a conjuring show. In physiology a physical chemist can find a wealth of problems waiting, crying out, to be solved. In the simpler—the so-called "exact" —sciences the field of work is, in some directions, already limited. One has even heard it hinted that organic chemistry may some day be "played out" and that its future fortunes will lie within the walls of the biochemical department. The economy and absence of pomp with which a living cell goes about its dozens of different reactions, should make a chemist with any sense of decency feel ashamed of his own crude methods. Here, in front of him (under a microscope) are mechanisms working with a precision and refinement which should be an object-

lesson and inspiration, and if at any time a chemist should feel that his own subject is beginning to be a little dull, beginning to provide no task worthy of his adventurous spirit, then let him come and take up one of the many problems which physiology will be glad to offer. But first—let me warn him—he must learn a little biology.

There are other sciences with which physiology needs and can claim an alliance. Years ago, in my first research, when I began to study the thermodynamics of muscle, I was moved to go and see, the professor of engineering at Cambridge. After all, the muscle was a machine, why not discuss it with an engineer? Professor Bertram Hopkinson, later a distinguished officer of the Royal Air Force in which he died, welcomed my coming and inquiries and gave me excellent thermodynamic advice. After all, why should he not? The muscle cell may be small, but it works just as well as a steam-turbine. This alliance with engineers has persisted, and throughout my work I have always found them glad to listen and to advise. The only rebuff I have ever had from an engineer was once, when as President of the Physiology section of the British Association it occurred to me at the organising committee to invite the engineers to hold a joint discussion with the physiologists. My "opposite number" was a designer of ships; he inquired, quite kindly but with

a smile which revealed his opinion of my state of mind, what subjects jointly we might discuss; I gaily replied that we might meet to consider the subject of sea-sickness, one which concerns not only the physiologist, not only the designer of vessels, but all who go down to the sea in ships. To my sorrow he continued to regard me as a lunatic and my plan was shattered. Just think what a joint discussion we might have had!

You may ask, why should physiologists and engineers feel themselves brothers? There is a sound philosophical reason. A fundamental principle of physiology is that the organism must be so arranged, its environment must be so adjusted, its own reactions so organised, that it continues to go on. It does not sound a very complicated principle, but nor does the statement that perpetual motion is impossible. The same principle is an inherent part of the philosophy of an engineer: a machine must continue to work, a structure must continue to play its part: "purpose" and "organisation" underlie the object of his studies as of ours. In this respect our methods of thought differ from those of other scientists, physicists and chemists, who deal with unorganised, purposeless matter. The engine studied by the physiologist shows an organisation and a purpose in just the same way as that designed by an engineer. In both cases the arrangement must go on.

This principle that the living cell must continue to function might seem so simple that no deduction could be made from it. Actually, in a mysterious way, as in the case of the second law of thermodynamics, important results can be deduced. Given certain physico-chemical properties of its structure, and of the fluids with which it deals, the principle that the living cell must continue—within limits—to function necessitates certain far-reaching conclusions which in some cases can be verified by experimental observation. In L. J. Henderson's work on this topic, to which I shall refer again in my last lecture, there is the germ of a new outlook on biology, a philosophical outlook avoiding both vitalism and mechanism, and keeping to the simple postulate, which few will dispute, that the organism must continue to function.

There is still a whole group of sciences with which I ought to deal. Of these, botany keeps a department of physiology of its own and it would be impudent for me to venture in its domain. Anatomy and the medical sciences have clearly an important connection with the work of physiologists: that is obvious enough, physiology has always been taught mainly to medical students, it is the basis of most real advance in medicine, it is intimately connected with pharmacology and pathology. Less obvious perhaps, but equally true, is the statement that

these other sciences can bring back gifts to physiology. Clinical experience of abnormal conditions is often a substitute for experiments which no man is able, or would dare, to perform. Clinical and physiological studies of the heart, by play and interplay, have led to a vast improvement of our knowledge of that organ. The urgency of diabetes continually pointed to the discovery of insulin, which was long believed to be present in the pancreas (indeed was given its name by Schafer from the Islets of Langerhans, long before it was discovered there) but which none could isolate; and the clinical symptoms of hyper- and hypothyroidism have led to our knowledge of the functions of the thyroid gland. All these things are well-known. In some places physiology is known as the "Institutes of Medicine."

For many years zoology has been chiefly concerned with the theory of evolution, with the inheritance of form, with the comparative structure and anatomy of animals. No doubt there is still much to be done in this direction, though sceptical people have been heard to affirm that the older type of zoology is getting somewhat threadbare. Certain, however, it is that some of the most important recent advances in zoology have come from the study rather of function than of form. Genetics and the physiology of reproduction afford obvious examples. As a meeting-ground for the sciences

one cannot choose a better place than the Marine Biological Laboratories at Plymouth or Wood's Hole. There one will find biologists expert in the form and development of animals, co-operating with others who are studying their environment, and the physical and chemical reactions of the animals to that environment. There one will notice biochemists investigating the processes that occur in the organs of marine animals, and physiologists employing the tissues which the sea supplies so amply, for the study of their special problems. The chief gift which zoology brings to physiology is in the multiplicity of its material. Physiologists are too apt to think in terms of the frog, the rabbit, the cat and the dog: sometimes they admit man also as an experimental animal. There are other and more beautiful creatures than these: some of them crawl on the bottom of the sea, some lead a more exciting life in the upper waters. Compared with land animals there is almost infinite variety of form and function and there is scarcely one of them that does not show some queer and unexpected property or trick. When we have come to an end of our resources, with our frogs and dogs and cats and men, when the tissue has proved too difficult for us, when our instruments are incapable of giving results of sufficient accuracy, all we have to do is to invoke the aid of the zoologist and to search for some animal or

organ which is more suitable for our investigations. Let me take an example. Most of our present knowledge of the mechanism of muscle has come from a study of muscular fatigue. At the present moment physiologists in many places are beginning to attempt to study nerve in the same way as muscle has been studied in the last few years. The frog's nerves and those of the cat and dog are little susceptible to fatigue: they need exceptional conditions before fatigue can be easily demonstrated. Consequently for a study of their energy changes and their metabolism they are singularly unsuitable. Now when you go to Plymouth the first thing you will see in the tank is a spider crab. He has a plentiful supply of legs, in each of which you will find an admirable nerve. These nerves show in a high degree the phenomena of fatigue and therefore supply a means of studying nerve-function, which in our home laboratories we lack. To take another example our present knowledge of certain important abnormal conditions of the heart, due mainly to Sir Thomas Lewis, really started from experiments made by Mines some fifteen years ago on the hearts of certain marine animals. The same is true of other animals than those of the sea, but it happens in the case of marine animals that physiology and zoology are not separate but work—with great advantage to both—in the same building. In respect of other

animals co-operation would be equally fertile, the gain to either party equally great.

You will see that I make large claims for physiology. It is a Key Industry but it does not need protection. As Professor Starling said of it, at Stockholm, it is "the best game in the world." It deals with matters of such personal importance to all of us, and it shows us such beautiful pictures and mechanisms and such an unlimited vista of unsolved riddles. It is at one moment so simple and matter of fact, and at another so involved with deep philosophical questions. Its progress requires adventurers from other sciences. The staid sober and respectable people had better stay at home: the crude methods, the tricks required to dodge the wilfulness of the living cell, the uncertainty of almost all the data that is printed in our textbooks, may seem to them unworthy of people trained in exact and reputable science. If, however, some adventurer from another laboratory wants to explore the unknown seas, let him come and investigate the problems of the living cell. He may return some day from his adventures a wiser and more cautious man. More likely he will remain a colonist in the new land which he discovers.

LECTURE VIII

Mechanism and Purpose

PHYSIOLOGY is supposed by many to be a severely practical subject. It is assumed to study those bodily functions of man which go amiss sometimes, so that the physician by knowing and understanding what is right and normal may be able to recognise and treat what is wrong and diseased. Though such an idea is very right and reasonable I would contend that physiology, can and should be very much more than this. In these lectures I have tried to show you certain other very practical applications of it: applications to industrial work, to athletics, to mountaineering, to muscular training, to ordinary everyday life: and at the same time to emphasise the wonder, beauty and completeness of the mechanisms with which the living body is filled. Apart, however, from these practical applications and these studies of living machinery, physiology has a wider, a more philosophical rôle to fill. There are many difficult and fundamental questions, questions which arise in most men's minds, to which an answer is continually being demanded. There is the age-long dispute between "vitalism" and "mechanism", the unanswered problem of whether

life can be "explained," or at any rate "described," in terms of physics and chemistry: the unsolved riddle of whether "mind" is simply a function of the nervous system: whether specific biological character depends only on specific chemical structure: whether apparently "purposeful" evolution and "useful" adaptation have other than a material basis: whether, if—as we believe—the mechanism of processes occurring during the dynamic equilibria of life can be described in ordinary scientific terms, those of growth, adjustment and repair, may some day be brought under similar rules. To what degree are intelligence and reasonable behaviour conditioned by the ordered functioning of the glands of internal secretion? It is quite obvious that these matters are not entirely unrelated. To what extent are emotions the result, to what extent the accompaniment, or the cause, of bodily changes? How far is human "character" the product of physiological functions and processes? Is there any reasonable physical basis for the continually recurring notions of "vital force" and "nervous energy?" The discussion of such problems is, in a sense, "unpractical"—it yields no immediate return, either in comfort, wealth or health. Perhaps even these questions are unanswerable. Yet it is only by attempting to answer them that physiology will attract those rarer intellects which can see the things which are too ob-

vious, or too subtle, for ordinary minds: only so can science attain those new and unexpected truths which at intervals will shake the foundations of our philosophy.

I cannot claim to be a philosopher, but these matters force themselves upon a biologist who tries, occasionally, to view the phenomena of life as a whole. I do not know even the words, nor am I acquainted with the technique of philosophy, and no doubt I shall be charged—quite justly—with imperfect logic and with giving the wrong names to things: though I hope I shall not offend any worse than the psychologists who talk of "nervous energy," or the philosophers who talk of "vital force," when they do not mean "energy" or "force" at all. Yet I feel so sure of two broad principles which should govern all biological thinking and investigation that I should be lacking in courage and honesty were I to neglect to bring them before you. The first is that there is no limit to the degree to which the mechanisms of life can be explored and elucidated by what are commonly called physical and chemical means: nature has erected no barrier beyond which "trespassers will be prosecuted," and arranged no desert into which it is profitless to go. The second is, that however far we get we shall still find "function," "adaptation," "organisation," "purpose," in the processes we explore: the pur-

pose may seem queer sometimes, the function may be unexpected: the adaptations may prove imperfect, but viewed as a whole they will be found to represent the best compromise available. Of this second principle, which is the basis of all biology, we may feel as sure as of the Laws of Thermodynamics: if we find apparent exceptions we must scrutinise our data more carefully: we shall not find "Nature" tripping. If we examine some of the lowly forms of life we may wonder what set them off developing in their particular queer way: we may reflect that, having started off on that one special path, perhaps by "chance" (an expression merely for our ignorance of the true cause), their further development along that path was probably inevitable: but, given the path, which may seem by our anthropomorphic standards, strange, the design and adaptation will be found to be wonderful, beautiful, complete. It is not easy to see why God wanted to create a sea-urchin, to crawl about on its quaint spikes on the bottom of the ocean: it does not seem to have any particular high function in His universe: it does not represent a step, so far as we can ascertain, to anything better: perhaps indeed it was just an amusing experiment. Granting, however, that He did want to make it—as indeed He obviously did—the design is wonderful and entrancing. That amazing organ, the Lantern of Aristotle, with its

wonderful system of levers and muscles, would be a work of genius even if erected from preformed parts: how much more when it developed by a process of growth, with all the rest of the animal, from a single cell. Its "water-vascular system," and the thousands of spikes on which it walks about, are scarcely less amazing. The sea is filled with creatures for which, equally, one can see no ultimate purpose, no reason why they ever started off on their long strange journey in evolution: complicated creatures, making the best of an impossible design: simple creatures, perhaps just fitting in to a "corner" that happened to be there: with amazing means of capturing their prey, or of dodging or "bluffing" their enemies. The dredge or the trawl may come up filled with multitudinous life, which will pour out kicking, flapping and struggling on the deck: to each unit, however small, there will be a design, a place in evolution, an infinity of adaptations and functions: yet the "purpose" of each animal as a whole, except perhaps as an exercise in skill, as an example of beauty of construction to a ridiculous design, as an experiment, it is impossible to guess: but the function and adaptability of each individual part are wonderful.

After all, is the "purpose" of the higher animals really any clearer? We are taught to think of the human race as a step in evolution: we imagine our-

selves to be the latest stage in the gradual upward path of "progress": to be the chosen vehicles of that new revelation; our "function" some would say is to leave the world wiser and better than it was when we came into it: can we be sure that we are right, or indeed that we understand the matter at all? Of all our individual functions, parts and organs, there is no question: each has its purpose, its design, often in the light of scientific investigation very clear and very beautiful: and they all work together, by physical and chemical means, in a world of energy and matter: but of ultimate purpose, as of ultimate reality, have we any means of judging? And if we are not sure of our own "purpose," our own destination, need it worry us that the purpose of our distant relatives on the land or in the sea is so obscure? The one thing of which we may be certain is that, given the animal, its organs and parts will be so arranged, its physical and chemical organisation so adapted, its molecules so built up and arranged, that it has the best chance of surviving and of reproducing its kind, under the changing conditions of its environment. In every detail this limited "purpose," this "function," this power of adaptation will be found.

We must beware of confusing our minds by too general an acceptance of the metaphysical notions of "progress" and "purpose." Based as these may

ultimately be on real and observable facts, great as, within limits, is their usefulness, their misuse may lead to most queer and unpleasant consequences and idolatry. There are some who know so much about the purposes of the Almighty, and it is these who are the most intolerant of the other beings He created. In a recent anti-vivisection controversy it was affirmed that "God never intended one of his creatures to profit at the expense of another:" which is a quaint deduction from tigers, sharks, or fleas: while a lady with a hypertrophied sense of justice prayed that a certain physiologist might, in the next world, be changed into a dog, so that he might be properly vivisected for his mistaken opinions. "Purpose" and "justice" are real and honorable notions, but they are not so simple as that. Their misuse originates from too far-reaching a deduction from the obvious phenomena of life. Seeing everywhere the adaptability of organs, the integration of functions, the inter-relations of parts, the uses to which things can be put, people searching for an easy explanation have put cause before effect, and attributed it all to a Divine Purpose suiting their own desires. And since desires and opinions differ as to what that purpose is there have been wars and struggles about it, intolerance and false deduction, cults and "fancy religions," "vitalism" and the reaction to it, "materialism."

Universal as physiology is, or should be, in its scientific applications and outlook, it must avoid unceasingly the danger of going beyond deduction from what can be experimentally observed. "Purpose" and "function" express real enough relations between the mechanisms of life, and the compass of physiology is the study of the mechanisms of life, in any form and by every means and device that Science offers. There are some—for example J. S. Haldane—who would complain that the very use of the expression "mechanisms of life" is in itself illogical, that it begs the question at issue. Are they "mechanisms," or is there something ultra-physical behind them? To me, if they are not mechanisms they must be miracles: there is no intermediate state. It is easy to become the slave of words, but I try to use the term "mechanisms" in the simplest possible way, merely as an expression for the organised capacity of a living creature for moving and changing things in the physical world of its environment. The living creature produces a great variety of physical, chemical and mechanical effects. The immediate effects we observe are all of a material kind. No "vitalist," however staunch, will deny that a living thing possesses mass, momentum, kinetic energy, or that it may be accelerated by what we call "force." The conservation of energy and the conservation of mass apply to it just as to other

material bodies. It produces heat from chemical energy, or it stores chemical energy from radiation absorbed. It liberates mechanical from chemical energy with a relatively high "mechanical efficiency," it produces electric currents, it takes in oxygen and food, it gives out carbon dioxide and water. Through its sensory organs the animal is aware of material changes occurring outside: all these have a physical or chemical basis: all of them must result in physical or chemical changes in the structures they affect. These are the things implied by the word "mechanisms," these are what the physiologist must needs study if he intends to face his task.

You have seen how "mechanistic" in a sense is the picture of the functions of the body which in these lectures I have brought before your eyes. It is obvious that the physical and chemical results of an animal's activity—work and movement, electric currents, heat, oxidation, transfer of messages to and fro—must have an immediate physical or chemical cause. It is inconceivable to most workers in physiology that at any stage they should finally be held up by anything save their own personal limitations —as unthinkable as a physical limit to space or time, as a simple equation without a solution. If a new factor be found it *must* be fitted in to the physical scheme of things: if it can be measured, it *must*

obey the quantitative laws of the exact sciences. No exception has been found—and it is the first article of a scientist's faith that no exception will be found. It is unimaginable that at some stage, suddenly, there should be a discontinuity in the material order of things. At intervals in history theological dogma and philosophical prepossession have attempted to curb the presumption of the human spirit in its belief that things can be understood and explained: but always in the end that belief and presumption have been justified. We can go on in our attack by physical and chemical methods, on the problems of life-phenomena. Some portions of the enemy's front are weaker than others: sound strategy suggests that these be attacked first: at intervals come great and resounding victories, which hearten us for the slow war of attrition that has mostly to be waged. Of one thing, however, the scientist is convinced, to him it is a matter almost of religious faith, that advance is possible, that given sufficient skill, courage and resolution and sufficient material resources, progress can be made, that there is no supernatural sentry standing outside some fortress to say to him "on ne passe pas." Of these presumptions of the scientist, and of his faith in his methods, you are indeed well aware: they may be right or wrong: to him it is inconceivable that they should be wrong. Of one thing only

he is assured, in one respect only he will admit no possibility of error, namely that there is no limit *in principle* to scientific advance by methods of observation and experiment. If he is wise—as he sometimes is—he knows full well the limitations of his own particular intellect, of his own particular methods: he may realise that the knowledge possessed by his generation is insufficient to solve some particular problem: but he will never admit that there is any absolute end to all things material beyond which it is inconceivable that his methods should apply. Physicists and Biologists are alike in this respect: both are certain, and experience tends to make them more certain, that there is no absolute limitation in principle to the powers of the human intellect in exploring the world, living or non-living, by means of observation and experiment. Granting this—and with one who will not grant it there can be no further argument—let us turn to another side of the picture.

To study these matters properly one needs the training and outlook, not only of the physicist and chemist, but of the biologist: and the biologist has a philosophy of his own, often unconscious, seldom fully realised, enshrined in words and ideas and methods of thought and action which are a necessity of his work. In the simpler, the so-called "exact," some would say the more fundamental

sciences, physics and chemistry, there is no place for these conceptions. In biology to talk of the "function" of an organ, the "purpose" of a reaction or adjustment, the "individuality" of an organism, the "co-ordination" of its parts, the "integration" of its functions, is perfectly good sense, based upon obvious and verifiable experimental facts. Throughout the realm of living nature we find an adaptation of means to ends. The ultimate "purpose" if there be one, is not visible: to the religious mind it may be revealed, but it cannot be verified by observation or experiment: the intermediate "purposes," however, are clear enough. It would be unreasonable to discuss the "instinct" of a molecule, the "co-ordination" of the parts of the solar system, the "rôle" of helium in the atmosphere, the "purpose" of crystalline structure, the "function" of water in the universe: it is not unreasonable, it is a plain expression of every day observation, to speak of the same factors in relation to a living system. There is clearly a persistent "effort" on the part of an organism to revert to a certain "normal" state. A man's weight may be constant for years, within perhaps 1 or 2 per cent., whatever—within limits—he does. If an animal be injured it proceeds—again within limits—to restore or regenerate its injured part. It may be difficult to fit these purposes and adaptations into a purely mechanistic philosophy: but because of that

difficulty to deny their real existence, as properties of a world containing living as well as non-living things, to suppose, as mechanists must do, that these are only ordinary properties of matter, is as unreasonable as the proverbial behaviour of the ostrich desiring to avoid the sight of things unpleasant.

A painting, a poem, a melody or a mathematical proposition, are all, in a sense, physical or chemical in nature: they require paint and canvas, ink and paper, air and sound waves for their manifestation. Is it reasonable, however, to regard a painting as *nothing* but paint and canvas, a poem or a mathematical proposition as *nothing* but ink and paper? Suppose we can explain in precise physical terms the working of the heart—does that tell us how it happens that the heart is so exactly suited to the needs of the animal it serves? One has only to study the physiology, and the anatomy of the muscular and circulatory system with sufficient care, with sufficient imagination and respect, and one finds all kinds of singular and purposeful adjustments, something quite different from the physics and chemistry of the mere contractile process by which energy is liberated and work done. In these purposeful adjustments and designs you will see, if only you approach the world of living phenomena with sufficient reverence and intelligence and with eyes sufficiently wide open, an organisation which is quite beyond the laws of

chance. To appreciate it properly a man requires the sentiment and training of a "biologist," some instinct to appreciate the organisation, the complexity and the consistency of living things, some natural humility in face of a great and perplexing problem. It is futile and childish to attribute it all to the great god "Chance," and his prophet "Natural Selection." One can trust this "biological" judgment, as in other matters one can trust the instincts of a physicist or an engineer: let us argue from "dimensions" that if such and such a mechanism is to work on a different scale of size it must needs change its properties in a corresponding way: and behold! if we examine it we shall find that Nature has worked out the mechanism as we have predicted.

There are three great principles among the laws of physics: that of the Conservation of Matter, that of the Conservation of Energy, and that known as the Second Law of Thermodynamics. In biology there are three not dissimilar principles, though they are not often so clearly stated: that of the Conservation of Species (to invent a name for it); that of organic evolution; and one which is emerging at the present day which might be called the "principle of adaptability." This last principle, in its lack of definition, in the means which it provides of evading any knowledge of the detailed mechanism, is analogous to the Second Law of Thermodynamics. The

Second Law tells us that whatever change we try to impose on a material system that reaction will go on which tends to resist the change. It tells us that in an isothermal system the "free energy" will tend to diminish: that in any isolated system the "entropy" will tend to increase. It asserts that by no means can the heat of an isothermal system be employed to do mechanical work. It implies that perpetual motion is impossible. All of which is clearly admitted and believed. But it has another and a more mysterious side. By juggling with it and with the physical characters of the bodies involved we can deduce all kinds of queer and unexpected relations between measurable experimental facts. The lowering of freezing point of a solution can be calculated from the heat of evaporation of the solvent: the fall of temperature when a strip of steel is stretched can be deduced from the coefficient of expansion of the steel with temperature: the change in solubility of a salt with pressure can be determined from the change of volume which occurs when the salt goes into solution. Strange deductions from the purely negative statement that perpetual motion is impossible! In recent years Professor L. J. Henderson of Harvard has been attempting to formulate and develop another and an almost equally simple law, applicable to biological systems: it implies merely that the organism is able, within

certain limits, to react to changes in its environment, to adapt itself to the demands that are made upon it. It is almost a matter of definition: a living unit is a system which *can* so react: otherwise it would not be able to live: the definition leaves its nature vague. Yet, accepting the physical and chemical characteristics of the environment (which is what we do in physics when making deductions by the aid of the Second Law), it allows us to predict all kinds of curious and unexpected things, which in fact are verified. The methods of prediction are not easy: but they have an almost romantic effectiveness. They have been applied hitherto only to a few cases, especially to that of blood and circulation: but there would seem, in principle, to be no reason why they should not be used on many other systems of the body, once data of sufficient quantitative accuracy have been acquired.

The principle involved is simple and matter of fact: yet it embodies, in a sense, all the philosophy that is necessary and sufficient to the biologist. As Henderson once said, biology and engineering are very closely akin: both deal with systems which must be assumed to "work." In both there is a set of physical and chemical parts, with "organisation" superimposed: nobody would suppose that the machinery of the engineer is based on laws other than these of physics and chemistry: at no stage has he to

invoke "vital force," or "nervous energy," or any other supernatural agency, to explain phenomena. So also in biology. The living cell *must* work in its own environment: otherwise it—and we—could not exist: its working is physical and chemical: its mechanisms must be so arranged that it will continue to work under a wide variety of circumstances: it possesses organisation and design: like a steam-turbine it has a "purpose": like a good automobile engine it has flexibility and power of adaptation. There are "intelligence" and "design" behind it: to recognise these is the province of the biologist—the student of life: there is mechanism inside it—to investigate that is the duty of the chemist, or physicist, or engineer. It is no more possible in a rational world to imagine a living cell without "adaptability" or "function" than to picture an engine without "design." Only a madman would attribute a telephone system purely to the laws of chance and the principle of natural selection: and only ignorance or fanaticism could attribute a living cell.

Sometimes people failing in courage, or patience, or skill, or having some preformed dogma to defend, think that they have come upon the limits of physical and chemical advance, that here or there a "vital force" or some other miraculous agency comes in: always, in the study of the phenomena of life, they will find, if they acquire a little more skill, or

exercise a little more patience, or display a little more resolution, or clear their minds of prejudice, that advance again is possible. The physical events which we perceive, movement, heat, chemical reaction, stimulus, can be analysed into other more fundamental things, which also we can perceive once we acquire the requisite mental and material tools; and these more fundamental things also are what we call physical and can be analysed and studied in their turn. But let us not fail to see the wood, because of the trees that are in it. A distinguished English chemist of my acquaintance maintains, in his innocence, that biochemistry is only ordinary chemistry carried on by appropriate ferments. It is like any skilled job—all so simple if you have only the requisite skill (or ferments). Equally it might be maintained that a painting is only paint and canvas: every molecule, every atom, in the picture is—or will be some day—intelligible: take any physical property you like of the paint and canvas and you can push its analysis back: the picture is impossible without the paint and canvas: and it can be destroyed in a few moments by simple physical or chemical means. Materialism is so easy and clear if one accepts its prejudices, and denies the existence of obvious facts: almost as easy—if not so consoling—as theological dogmatism. Most people, however, are not really deceived by either. Most rational folk

can be trusted to steer a safe middle course. The fundamental thing is the picture itself, the organisation of the paint, the adjustment of the colours, the purpose of its several parts. We may agree that, to become the complete artist, it is necessary to study the properties of paint and canvas, to reflect on the nature of colour, light, and shade, to observe the behaviour of material things: equally to become the complete biologist it is necessary to study the physics and chemistry of the events and materials which make up life. There is no limit to the physics and chemistry, no new and supernatural agency will appear: but all the time we shall find organisation, adjustment, purposeful response, adaptation, intelligence and persistence; and to refuse to recognise these things is to deny those very experimental facts of which, as observers of Nature, we are really certain.

The apostles of Natural Science are little given to reflecting on first causes and on the nature of things: perhaps they are afraid of being rebuked by professional philosophers for their ignorance of the proper words, and for not abiding by the accepted rules. It is a pity, for if they cultivate too closely their own little patch they will lose the inclination to climb the neighbouring hill, to see their patch in its proper proportions, and to enjoy the romance of a larger landscape. After all, one of the best motives

for the study of Nature is the mental enjoyment and the spiritual satisfaction which it brings. Science has proved, and will continue to prove, useful in a material way in alleviating man's lot, in curing disease, in prolonging and beautifying life: there are few investments more profitable than provision for those who have the skill and persistence required for the analysis of natural phenomena, whether in biology or in the physical sciences. It is easy, however, like Martha, to be so busy about much serving in scientific laboratories that one sees only a little corner of the whole: humanity owes much, admittedly, to the assiduous labours of its Marthas, but little advance, spiritual, mental and material, could have been achieved, had there been no Marys to listen and reflect on the bigger things. One needs at intervals, to take the wider view, and to ponder on the fundamental riddles. One will not try, if one is wise, to formulate too precise and definite a creed: the history of creeds should be a sufficient warning: but one can, and should, attempt, in a humble way, to see things as a whole. And in biology to see things as a whole is to recognise, on the one hand that there is no limit to the physical and chemical analysis of living mechanism, on the other, no end to its power of synthesis and adaptation into the complete and intelligent, the beautiful and wonderful living creature.

In the minds of most of mankind there lurks a desire for a religious, or at any rate for a mystical interpretation of life. This religious instinct is a very real thing, and whether expressed openly in religious observance, or merely—as a very distinguished biochemist once said to me—in the sentiment that "there is something somewhere" which does not fit into the mechanistic outlook on the world, it tends to colour our view of natural phenomena. Few people have much acquaintance with the methods of what is technically called "philosophy," but most thinking people have developed or acquired some kind of religious interpretation of the universe. Few great things have been done without some attempt to satisfy this religious instinct. During the advance of science, especially in the last few centuries, again and again there has arisen a struggle, often bitter and prolonged, between the protagonists of the religious practices of the time and the apostles of scientific method: and always, in the course of years, men have come to realise that there is really no fundamental contradiction between the religious *interpretation* of phenomena as a whole, and the detailed *description* of how they actually occur. It is sure that many of the precise and dogmatic statements of organised religion can face no analysis by the scientific spirit: nor can a demand for an unreasoning faith in an unreasonable creed: while it

is true on the other hand that the dogmatic assertiveness of some scientists, and the credulous materialism of others, must alienate many serious thinkers who are genuinely striving to see things as a whole, and without prejudice. Were there any chance—as Haldane says—of an absolute division between those, on the one hand, who hold with a religious outlook on the world, and those, on the other, who study and interpret natural phenomena by the methods of observation and experiment, then the majority of mankind (at any rate of English speaking mankind)—quite rightly—would be on the side of religion: but there is no such chance. The instinct which sees the human qualities of purpose, goodness and intelligence in all natural phenomena, living and non-living, and projects them into some supernatural being whom it calls God, is not in its nature far removed from the spirit which recognises function and adaptability as properties of all life; while the mysticism which views the material world as a manifestation of some deeper underlying reality is not unlike some of the developments of modern, theoretical physics. Truth can be pursued by many means, and if we are right in our belief that a reasonable, consistent view of the world is possible, even though we ourselves may never conceive it, then there can be no ultimate conflict between those who pursue the truth, from whatever aspect, critically and care-

fully, without prejudice and with sufficient patience, reverence, and imagination.

Living Machinery, the title of these lectures, may have seemed to some of you to convey a challenge. To a degree it does: I have ventured to present to you the workings of some of the important organs of the body as though their study were simply a branch of engineering. You have seen the nervous system likened to a telephone exchange: the messages in the nerve-fibres are "waves of electro-chemical change:" the frequency and path of these messages determine the nature of response. The muscles are little self-contained engines, consuming fuel and liberating energy: an athlete's behaviour can be expressed in terms of horse-power and resistance, lactic acid and oxygen: movement of all kinds in living things is shown to be of the same universal character, depending on molecular changes. The behaviour of many organs of the body, with all their wonder, is in some respects no more difficult to understand, than the working of a Ford car: a child can perform and interpret some of the experiments by which their behaviour is made clear. All this is a challenge, but a simple one: not, as my Apologia in this lecture will have shown you, to any fundamental beliefs: only to the accepted method of regarding and learning about the body.

The body is one of the most beautiful and amazing

machines in the world, filled with intricate devices, cunningly adjusted, wonderfully adapted. A generation ago it was thought to be rather a gruesome affair, this living machinery: a matter for the hospital or dissecting room. Today it is beginning to be recognised that a certain knowledge of the mechanism of bodily existence is essential to any reasonable culture and education: even so, however, it is often supposed that the simple dissection of a dead animal is sufficient for most purposes. I have endeavoured, in these lectures, to present another point of view, that of the experimentalist as distinguished from the observer. It is possible to experiment with the body—with the human body—: to measure the results, often with considerable accuracy: and to fit them into a reasonable scheme. People are interested in these experiments, much more than in the form of the dead rabbit or dog-fish: and—especially if they are young—they often like to have them made upon themselves. I believe that the right way to interest people in physiology is to encourage them to make experiments on themselves: to learn what goes on in their own bodies: and so, if they be minded, to lead them on to the more fundamental branches of the subject. That is why I have continually described the body in engineering terms: people, especially men and children, are interested in machines: they like to take things apart to see how they work. There

is nothing "horrid" about the body, nothing "gruesome" or "unpleasant," and there is certainly nothing, in discussing its machinery, which need make us adopt too "mechanistic" an outlook on life. Mechanisms there are, but filled with complex and ever-present effort and growth: material devices, but filled with function and adaptability: physical and chemical processes, but bound up with a mysterious kind of intelligence and purpose: all of which is as wonderful in the beauty of its mechanism, as it is mysterious for the problem of its ultimate end.

Doubtless some of you have expected me to deliver judgment between "vitalism" and "mechanism." For many years I have tried to do so and failed. I find that it is as impossible as to answer the historic question, "Have you given up beating your wife?" Both "vitalism" and "mechanism" seem to me to be wrong and unscientific: both to be unreasonable deductions from obvious facts. To ask me to assent to "vitalism" is to invite me to believe in a miracle, in a complete discontinuity in Nature, in a ghost producing material effects. It may be possible, if you shut off half your brain, to give an emotional assent to the hypothetical existence of ghosts, or spooks, or ectoplasm: but not if you set out to track them down, and to study their properties and behaviour: then you find that there are no such things at all. It is not difficult, if you

allow your imagination to run riot, to talk about "vital force": but if you try to locate it you find it isn't there. To invite me, on the other hand, to agree to "mechanism" as an explanation of life-phenomena, is to ask me to bury my head in the sand, and to pretend that things are not there when I know they are. The dogmas of materialism are as impudent as those of medieval theology: both are unworthy of reasonable men who are searching humbly for the truth.

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